Green-tailed Towhee (*Pipilo chlorurus*): A Technical Conservation Assessment

Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project

March 30, 2006

Robert C. Dobbs
621 Parker Street
Fort Collins, Colorado 80525

Peer Review Administered by
Society for Conservation Biology

Dobbs, R.C. (2006, March 30). Green-tailed Towhee (*Pipilo chlorurus*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/greentailedtowhee.pdf [date of access].

Acknowledgments

I thank Brian Gibbons, Gretchen Jehle, and Tony Leukering for providing unpublished data and discussing their observations and knowledge of green-tailed towhee breeding ecology in Colorado. I am grateful to Doug Faulkner, Glenn Giroir, Hugh Kingery, Arvind Panjabi, and numerous USFS employees, Dave Bradford, Brian Cox, and Skip Fisher in particular, for responding to various queries and requests for information. Special thanks to Paul Doherty for helpful discussion of demographic analysis and matrix population models, Cameron Ghalambor for providing access to office resources, Jim Lowe for providing unpublished data from the Cornell Nest Record Card Program, and Paul Martin for sharing unpublished data and observations. Thanks to Gary Patton for helpful editorial assistance and guidance, and Gretchen Jehle, Steve Sheffield, and an anonymous reviewer for valuable comments on the manuscript.

Author's Biography

Robert C. Dobbs is a field ornithologist, currently free-lance and based in Fort Collins, Colorado. He holds B.Sc. (1995, Zoology, University of Arkansas) and M.Sc. (2001, Biological Sciences, Illinois State University) degrees, and he has published over 20 peer-reviewed papers on various aspects avian biology. His field research on green-tailed towhees, conducted over several years in northern Arizona and elsewhere, added significantly to its Birds of North America species account, which he and collaborators published in 1998. His current research focuses on resource partitioning and specialization within Andean bird communities, and habitat use and foraging ecology of Neotropical-Nearctic migrant songbirds during the nonbreeding season.

Cover Photo Credit

The green-tailed towhee (*Pipilo chlorurus*). © Greg Lavaty, photographer. Used with permission.

Summary of Key Components for Conservation of the Green-tailed Towhee

Status

The green-tailed towhee (*Pipilo chlorurus*) is a characteristic species of montane shrublands (e.g., shrubsteppe, foothill shrubland, woodland-shrub savanna) in the southern Rocky Mountains. Although a great deal of uncertainty is associated with the data, green-tailed towhee populations appear to be stable rangewide and within USDA Forest Service Region 2, which holds a significant portion of the species' overall population.

Primary Threats

The major threat to green-tailed towhee populations in Region 2 is the long-term degradation of shrub-dominated habitats through the effects of fire suppression, livestock grazing, and the introduction of non-native annual grasses. The interaction of these factors over the past century has reduced the heterogeneity of shrubland habitats at local and landscape scales. In lower montane and foothill areas, intense fire suppression and livestock grazing facilitate the uniform invasion of woody vegetation (i.e., sagebrush in shrubsteppe, junipers in foothill shrubland, and pines in shrub-pine savanna), which reduces the mosaic quality of shrubland habitats that green-tailed towhees prefer. Combined with dense, even coverage of introduced non-native grasses, these factors also promote intense wildfires that remove all shrubs and prevent shrub regeneration in burned areas, making these habitats unusable by green-tailed towhees. In mid-high elevation coniferous forests, fire suppression has decreased the variation in post-fire seral stages, and thus decreased habitat availability on a landscape scale. Mining and oil and gas development represent important mechanisms of habitat fragmentation on the shrubsteppe landscape, while off-road vehicle recreation and urban development increasingly threaten to degrade and fragment shrubland habitats, especially in the foothills of the Colorado Front Range.

Primary Conservation Elements, Management Implications and Considerations

Management practices that reduce grazing pressure, reintroduce fire to the landscape, and prevent the introduction and invasion of non-native grass species will likely be most effective in maintaining and restoring the mosaic quality of native shrubland habitats. These management practices thus are most likely to have the greatest benefits to green-tailed towhee populations in Region 2 and elsewhere. Nonetheless, due to a lack of information on green-tailed towhee population biology and its response to management, both generally and in Region 2, rigorous scientific research is of critical importance to understand the conservation needs and best management practices for this species. In particular, research investigating this species' response, in terms of both population density and productivity, to fire and grazing management practices and the effects of anthropogenic disturbance and habitat fragmentation are badly needed.

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INTRODUCTION

This conservation assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2; **Figure 1**), USDA Forest Service (USFS). The green-tailed towhee (*Pipilo chlorurus*) is the focus of an assessment because it is classified as a Management Indicator Species (MIS) on one or more national forests in Region 2. Within the National Forest System, a MIS can serve as a barometer for species viability at the forest level. By monitoring a MIS, managers can 1) estimate the effects of planning alternatives on fish and wildlife populations (36 CFR 219.19 (a) (1)) and 2) monitor the effects of management activities on species via changes in population trends (36 CFR 219.19 (a) (6)).

This assessment addresses the biology, ecology, conservation status, and management of the green-tailed towhee throughout its range in Region 2. The broad nature of the assessment leads to some constraints on the specificity of information for particular locales. That is, given the limited information available from field studies and its origin from throughout the species' range, only limited inference can be made for specific situations within Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

This species conservation assessment is designed to provide land managers, biologists, and the public with a thorough discussion of green-tailed towhee biology, ecology, conservation, and management. The assessment is based on current scientific knowledge. Assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussions of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop prescriptive management recommendations. Rather, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e.,

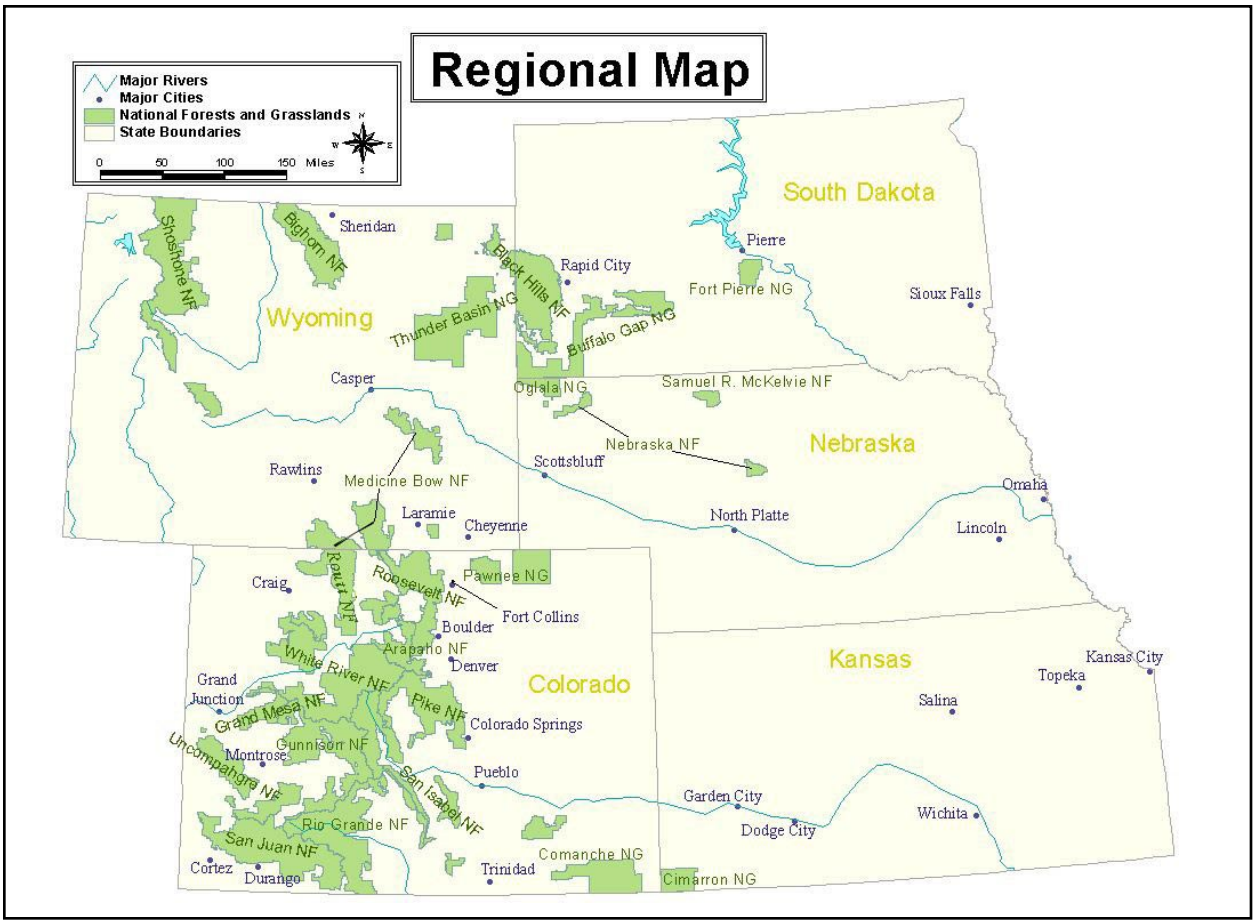

Figure 1. USDA Forest Service national forests and grasslands (map courtesy of USDA Forest Service, Region 2).

management implications). This assessment also cites management recommendations proposed elsewhere and examines the success of those recommendations that have been implemented. Potential and known effects of management on the green-tailed towhee may therefore be recognized and used by managers to direct land management decisions.

Scope

The green-tailed towhee conservation assessment examines the biology, ecology, conservation status, and management of the species with specific reference to the geographic and ecological characteristics of USFS Region 2. Although much of the literature on the green-tailed towhee originates from field studies conducted outside of this region, this document places that literature in the ecological and social context of the central and southern Rocky Mountains. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of the green-tailed towhee in the context of the current environment rather than under historic conditions. The evolutionary environment of the species is considered in conducting the synthesis, but it is placed in a current context.

In producing the assessment, I reviewed refereed literature, non-refereed publications, research reports, and unpublished data accumulated by resource management agencies and others. Not all publications on the green-tailed towhee were referenced in the assessment, nor were all available materials considered equally reliable. While this assessment strongly emphasizes refereed literature, I also cite unpublished data that has only recently become available from within Region 2. These unpublished data are of great importance to our understanding of the green-tailed towhee's biology in Region 2 and throughout its range. Nevertheless, I considered non-refereed publications and reports, as well as unpublished data, with respectful skepticism and cited them only when better information was not available elsewhere.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge in which competing ideas regarding how the world works are measured against observations. However, because our observations and descriptions of the world are always incomplete, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). It is often difficult, however, to conduct critical experiments in the ecological sciences, and thus observations, inference, good thinking, and models often must be relied upon to guide the understanding of ecological relationships (Hilborn and Mangel 1997).

In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches (e.g., modeling, critical assessment of observations, inference) were accepted as sound approaches to understanding the green-tailed towhee. This species is remarkably little studied, and much of what is known of its biology has come to light only recently. The only green-tailed towhee studies conducted in Region 2 have been completed very recently, and we cite these important, yet unpublished, contributions. Still, very little information is available on the green-tailed towhee's response to habitat alteration or habitat management, an important part of this assessment. We thus evaluated conservation and management information developed for ecologically similar species that breed in montane shrubland and sagebrush habitats, placing this information in the context of the green-tailed towhee and Region 2.

Publication of Assessment on the World Wide Web

To facilitate use of these species conservation assessments, they are being published on the USFS Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, it facilitates their revision of the assessments, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer-reviewed prior to release on the Web. Through a process administered by the Society for Conservation Biology, this report was reviewed by two recognized experts to provide critical input on the manuscript. Peer-review was designed to improve the quality of communication and to increase the rigor of the assessment.

Management Status and Natural History

Management Status

The Natural Heritage Program considers green-tailed towhee populations "secure" at global (G5) and national (United States; N5) levels (NatureServe 2004). Throughout most of the species' breeding range, populations at the state level are "apparently secure" (S4; Montana, New Mexico, Oregon, Texas, Utah) or "secure" (S5; Colorado, Idaho, Nevada, Wyoming). Exceptions are Arizona and Washington, where breeding populations are considered "vulnerable" (S3) and "critically imperiled" (S1), respectively (NatureServe 2004). State status rankings of winter populations in the United States are "apparently stable" (S4) (NatureServe 2004); no information is available on the status of winter populations in Mexico.

The green-tailed towhee is a Partners in Flight (PIF) "stewardship species" in the Intermountain West avifaunal biome, which comprises much of the species' range in Region 2 and holds 92 percent of the species' breeding population (Rich et al. 2004). As such, PIF considers the green-tailed towhee in need of long-term planning and responsibility in those areas, with the goal of maintaining current populations (Rich et al. 2004). Among PIF state bird conservation plans, the green-tailed towhee is a priority species, at some level, in montane shrub habitats in a number of states (e.g., Idaho, Montana, New Mexico), but it receives no such status in a number of others (e.g., Arizona, Nevada, Utah). Within Region 2, the green-tailed towhee is a high priority species in mountain shrubland in Colorado (Beidleman 2000), but it is not considered a priority species in Wyoming (Nicholoff 2003). The green-tailed towhee does not breed, and is only a rare migrant, in other states within Region 2 (i.e., South Dakota, Nebraska, Kansas), none of which currently have PIF bird conservation plans.

Within USFS Region 2, the green-tailed towhee currently serves as a MIS on the San Juan National Forest; it was recently removed from the Pike-San Isabel National Forest MIS list (USDA Forest Service 2005). The green-tailed towhee was selected as a MIS on the San Juan National Forest because it is a characteristic species of mountain shrub communities, a unique habitat of limited distribution (Ecosphere Environmental Services 2004).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Regulatory mechanisms have not been developed specifically for the green-tailed towhee, but a number of existing laws protect migratory birds and, to a lesser degree, their habitats. Like all migratory birds, green-tailed towhee individuals and populations are protected by the Migratory Bird Treaty Act (MBTA) of 1918, which prohibits the take of protected birds. "Take" is defined as to "pursue, hunt, take, capture, kill, attempt to take, capture or kill, possess, offer for sale, sell, offer to purchase, purchase, deliver for shipment, ship, cause to be shipped... or export, at any time, or in any manner, any migratory bird... or any part, nest, or egg of any such bird" (16 U.S.C. 703; http://laws.fws.gov/lawsdigest/migtrea.html). An amendment to the MBTA (P.L. 95-616) further specifies that the federal government take "measures to protect identified ecosystems of special importance to migratory birds against pollution, detrimental alterations, and other environmental degradations." With respect to habitat on federal land, the National Environmental Policy Act (NEPA) of 1969 requires that any federal agency formally consider environmental impacts of a proposed action, including unavoidable adverse environmental effects, alternatives to the proposed action, and the relationship between short-term human use and long-term productivity of the environment. The National Forest Management Act (NFMA) of 1976 specifically directs USFS land and resource management plans to "provide for a diversity of plant and animal communities."

Although the MBTA appears to be adequate in protecting individuals and, to a degree, populations of the birds themselves, the major threats to the long-term health of the green-tailed towhee are habitat loss, degradation, and fragmentation. It appears, for example, that existing laws may not be effective in minimizing the decline of shrub-steppe, an important green-tailed towhee habitat, on federal land (Knick et al. 2003). Moreover, conservation of the green-tailed towhee may also depend on privately-owned land (e.g., foothill shrub habitat), which generally is not subject to regulation as is federal land.

No management or conservation plans have been designed specifically for the green-tailed towhee. Nevertheless, within Region 2, the Colorado PIF bird conservation plan identifies a number of human

activities as potential conflicts with green-tailed towhee viability, and it suggests a number of management recommendations. Colorado PIF recommends conducting breeding season surveys for green-tailed towhees before planning habitat alterations (e.g., herbicide treatment, mechanical alteration, burning) in mountain shrublands. If habitat alteration does occur, Colorado PIF recommends (1) creating a landscape-scale mosaic of altered and unaltered habitat, (2) preventing the invasion of exotic plants, (3) scheduling any prescribed burning prior to the birds' arrival in early spring, and (4) leaving numerous small patches of unburned shrubs to maintain breeding habitat (Beidleman 2000).

Both the Colorado and Wyoming PIF bird conservation plans outline management issues and practices to conserve the shrubland habitats that are vital to green-tailed towhees in Region 2. These management strategies focus on maintaining landscape-scale mosaics of native plants of different age classes and at different densities, minimizing fragmentation, preventing the invasion of exotic plant species, and managing the land responsibly with respect to grazing and burning (Beidleman 2000, Nicholoff 2003).

Biology and Ecology

Description and systematics

The green-tailed towhee is a large sparrow (length 18 cm; mass 29 g) with a long, greenish tail. The sexes are monomorphic and largely monochromatic, although some females have duller plumage than males. Adult plumage is distinctive, characterized by a reddish crown and gray face and breast, which contrast strongly with white supraloral spots, submoustachial stripes, and throat. Yellow-green edging of wing and tail feathers contrasts with the solid olive green upperparts and grayish underparts of adults. Juveniles are mainly dusky brown on the head and upperparts, and white below with brownish flanks; they show extensive black streaking on the crown, nape, back, and underparts. As juveniles age, streaking disappears from the back and underparts, and yellow-green edging of wing and tail feathers becomes apparent. Given an adequate view, an adult green-tailed towhee is not likely to be confused with any other species north of Mexico. The streaky, brownish appearance of juveniles is generally similar to that of numerous smaller sparrows and, especially, juvenile spotted towhees (*Pipilo maculatus*). However, the latter typically shows two pale wingbars.

The green-tailed towhee is monotypic and shows no geographic variation. Within the genus *Pipilo*, which consists of eight species, the green-tailed towhee is most closely related to the spotted, eastern (*P. erythrocephalus*), and collared (*P. ocai*) towhees; it is distantly related to the "brown towhees" (Abert's [*P. aberti*], California [*P. california*], and canyon [*P. fuscus*] towhees) (Zink 1988, Zink and Dittmann 1991). The green-tailed towhee occasionally hybridizes with the spotted towhee (see photo in Sibley 1994), with which it occurs sympatrically over much of the western United States, including Region 2.

Distribution and abundance

Green-tailed towhees breed mainly between 1,400 and 3,200 m elevation throughout much of the Rocky Mountains, Great Basin, and Sierra Nevada of the western United States (Dobbs et al. 1998). The species breeds from southeastern Washington south through Oregon (east of the Cascade Mountains), east across southern Idaho, and north into south-central Montana. They occur throughout the Great Basin, west to the coastal ranges of northern California and the Sierra Nevada of central California, and east to Colorado's Front Range of the Rocky Mountains. Southward, the species breeds in southern California, east across southern Nevada and the Colorado Plateau, and south through central Arizona to southern New Mexico and the Davis Mountains in western Texas (Dobbs et al. 1998). A short to medium-distance migrant, the green-tailed towhee winters from the central California coast south and eastward throughout the southwestern deserts of southern California, southern Nevada, southern Arizona, southern New Mexico, and east to central and southern Texas. In Mexico, the species winters throughout Baja California, on the Pacific slope of mainland Mexico south to Jalisco, Michoacán, Distrito Federal, and Puebla, and on the Atlantic slope in Tamaulipas (Dobbs et al. 1998). Green-tailed towhees wander casually throughout eastern North America, mainly in winter (Dobbs et al. 1998).

The green-tailed towhee is a common breeding species in appropriate habitat in Region 2. Green-tailed towhees are present in Wyoming from May through September (extreme dates 30 April-23 December; Dorn and Dorn 1990) and are thought to breed in appropriate habitat virtually throughout that state (**Figure 2**; Cerovski et al. 2004). Recent survey work by Rocky Mountain Bird Observatory (RMBO) provides the only detailed distribution data for Wyoming (**Figure 3**, **Figure 4**, **Figure 5**; Faulkner 2005).

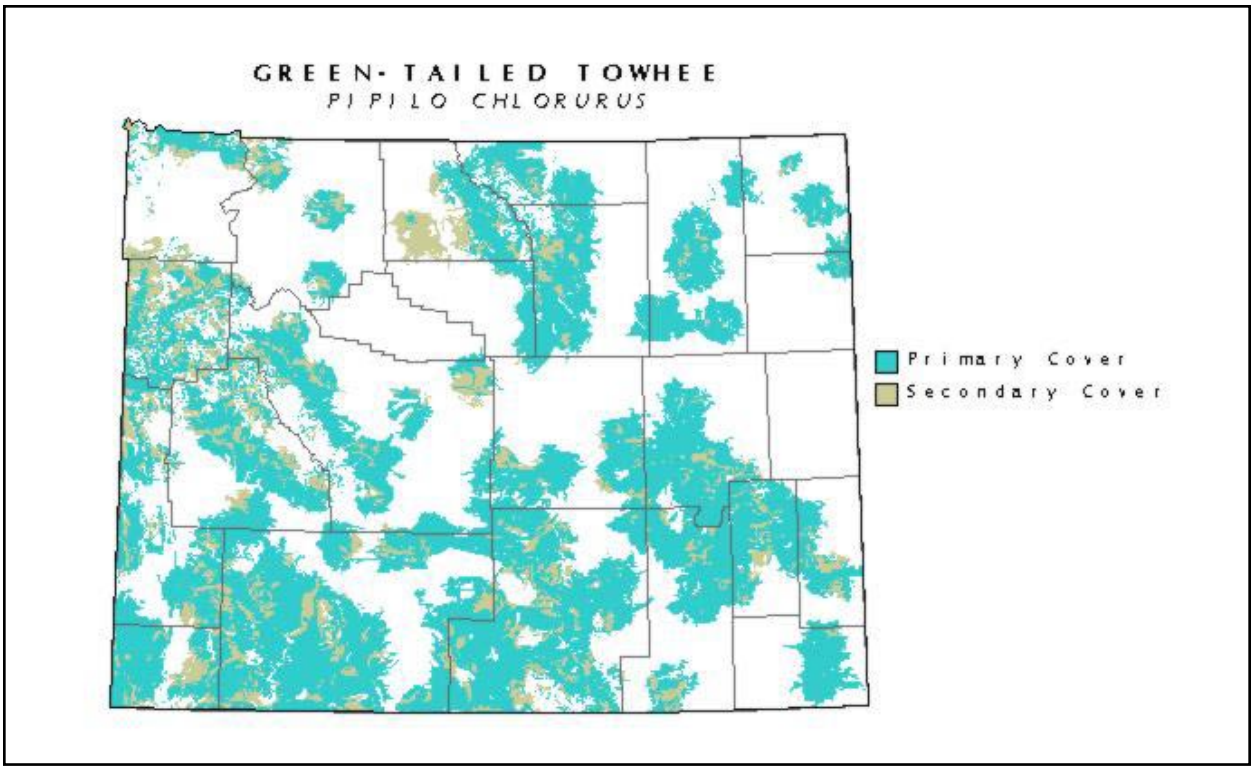

Figure 2. Distribution of green-tailed towhee breeding habitat in Wyoming, as modeled by the Wyoming GAP project (online: <http://www.wygisc.uwyo.edu/wbn/atlas>).

Although green-tailed towhees were previously suspected of breeding in the Black Hills of extreme western South Dakota (Rising 1996), extensive breeding season surveys in recent years by RMBO have failed to find evidence of the species (A. Panjabi personal communication, October 2004.

In Colorado, green-tailed towhees breed east to the Mesa de Maya in the southeast and in appropriate habitat throughout the foothills of the Front Range and westward through the state (**Figure 6**; Righter 1998). It is one of the most numerous breeding species in Colorado and is most abundant on the western slope, which has more suitable habitat than the eastern slope (Righter 1998). The species is typically present in Colorado from late April to early October (Andrews and Righter 1992). Green-tailed towhees rarely overwinter in Region 2, but one to three birds are found wintering in Colorado each year, usually near the base of the Front Range foothills, on the eastern plains, or in low western valleys from Eagle and Mesa counties southward (Kingery 1995, Truan and Percival 1996, 1997, 1999, 2000, 2001, 2002, Percival et al. 2003, Wood and Faulkner 2004).

Breeding Bird Survey (BBS) data suggest that the densest breeding populations of green-tailed towhees are in western Colorado, northeastern Utah, and in the central Sierra Nevada and montane areas of southern California (**Figure 7**; Sauer et al. 2004). Although green-tailed towhees may be poorly sampled by BBS methods in many areas and their population density may not be fully represented by BBS maps, BBS data confirm western Colorado as a breeding stronghold.

The green-tailed towhee is a rare migrant in the eastern portion of Region 2. It is a casual visitor (eight records) to the Black Hills region in South Dakota, mainly during spring (seven records, 8-30 May; Tallman et al. 2002). In western Nebraska, the green-tailed towhee is considered a rare regular spring migrant (33 records, 25 April-6 June) and a rare casual fall migrant (11 records, 6 September-16 October) (Sharpe et al. 2001). The species is a rare spring migrant (27 April-23 May) in southwestern Kansas (Thompson and Ely 1992).

Population trends

Breeding Bird Survey data suggest that green-tailed towhee breeding populations are stable overall and within Region 2 (**Table 1**; Sauer et al. 2004). Note, however, that state and regional variation in

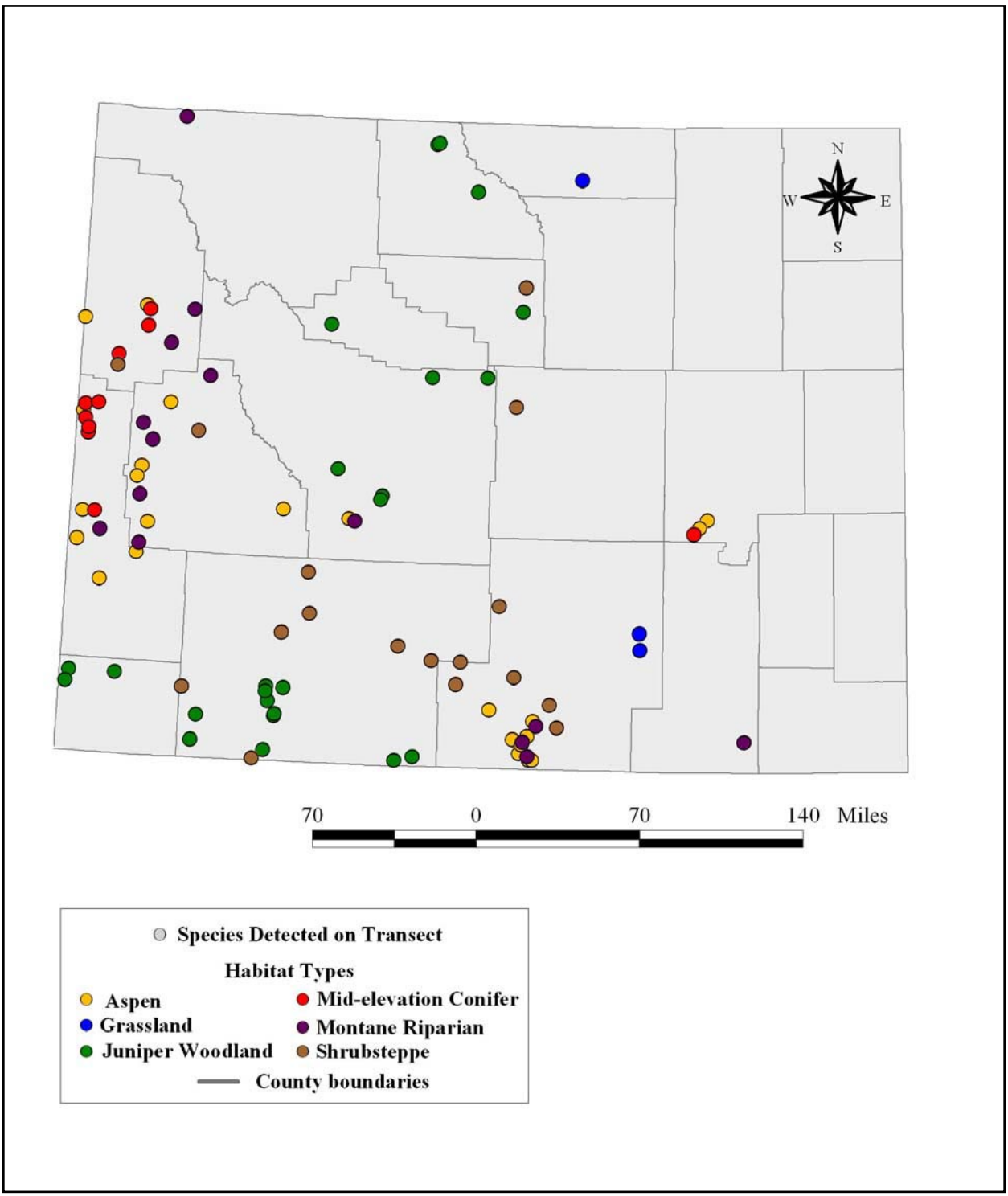

Figure 3. Habitat-stratified distribution of green-tailed towhee detections on point transects throughout Wyoming (Faulkner 2005; map courtesy of RMBO).

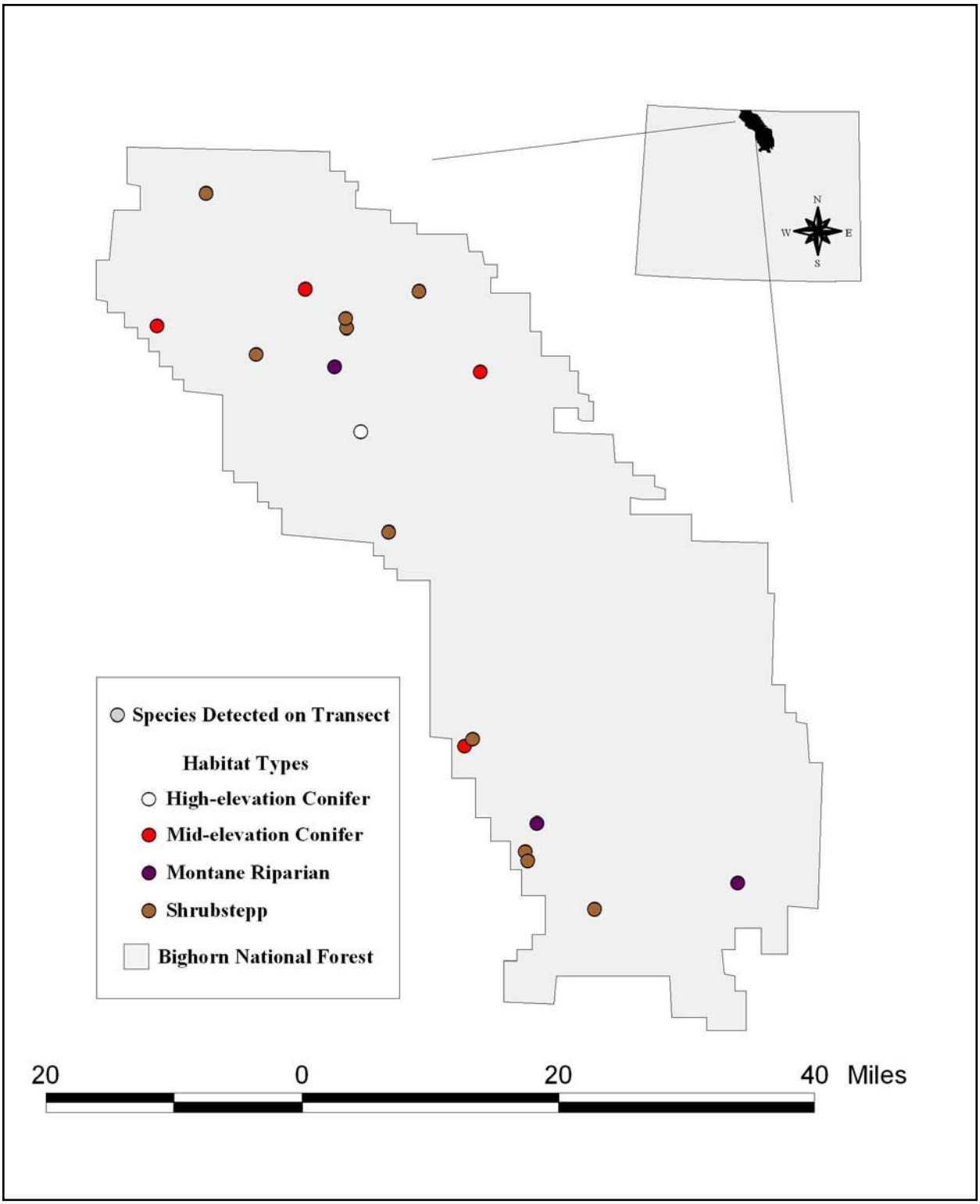

Figure 4. Habitat-stratified distribution of green-tailed towhee detections on point transects in Bighorn National Forest, Wyoming (Faulkner 2005; map courtesy of RMBO).

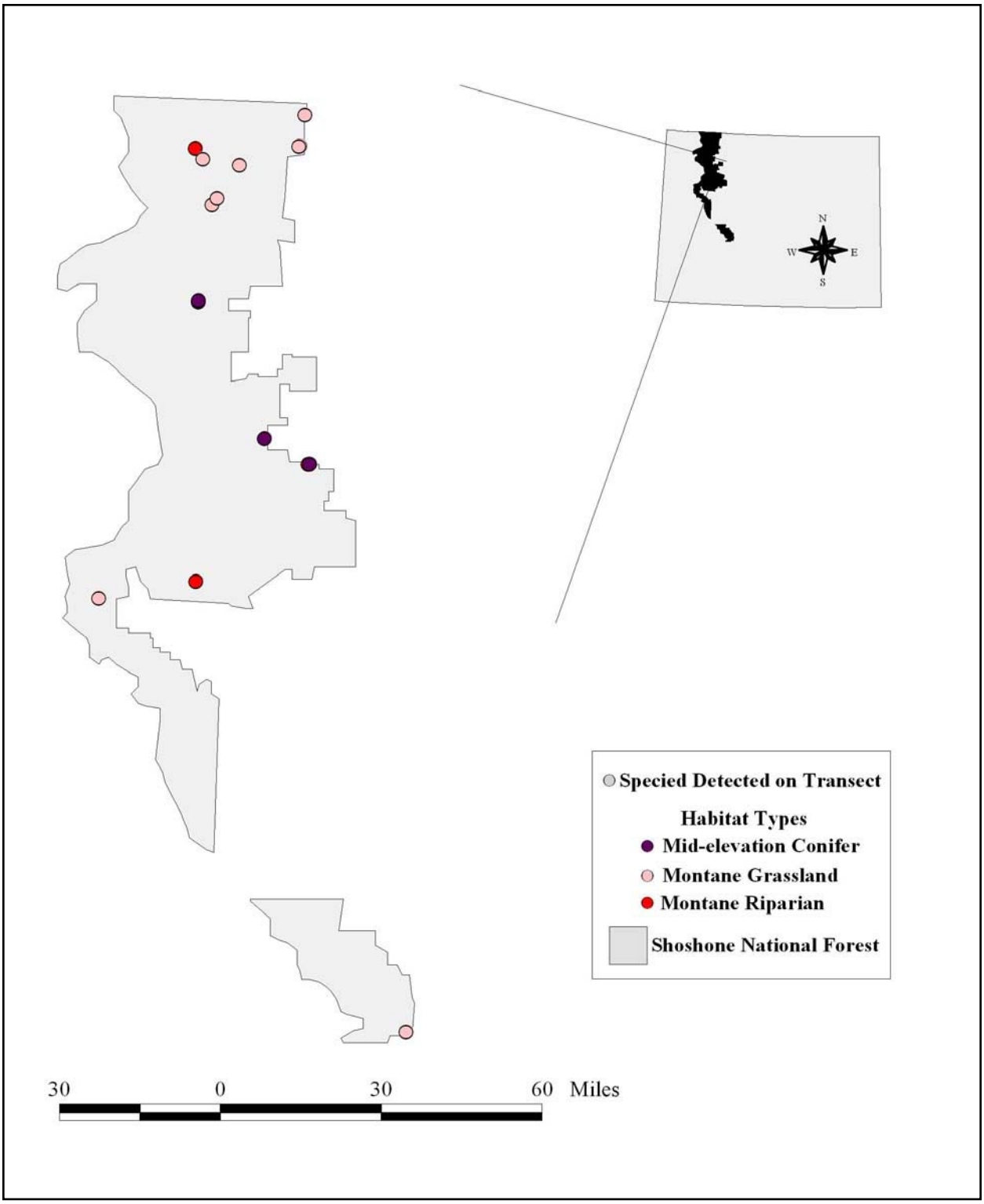

Figure 5. Habitat-stratified distribution of green-tailed towhee detections on point transects in Shoshone National Forest, Wyoming (Faulkner 2005; map courtesy of RMBO).

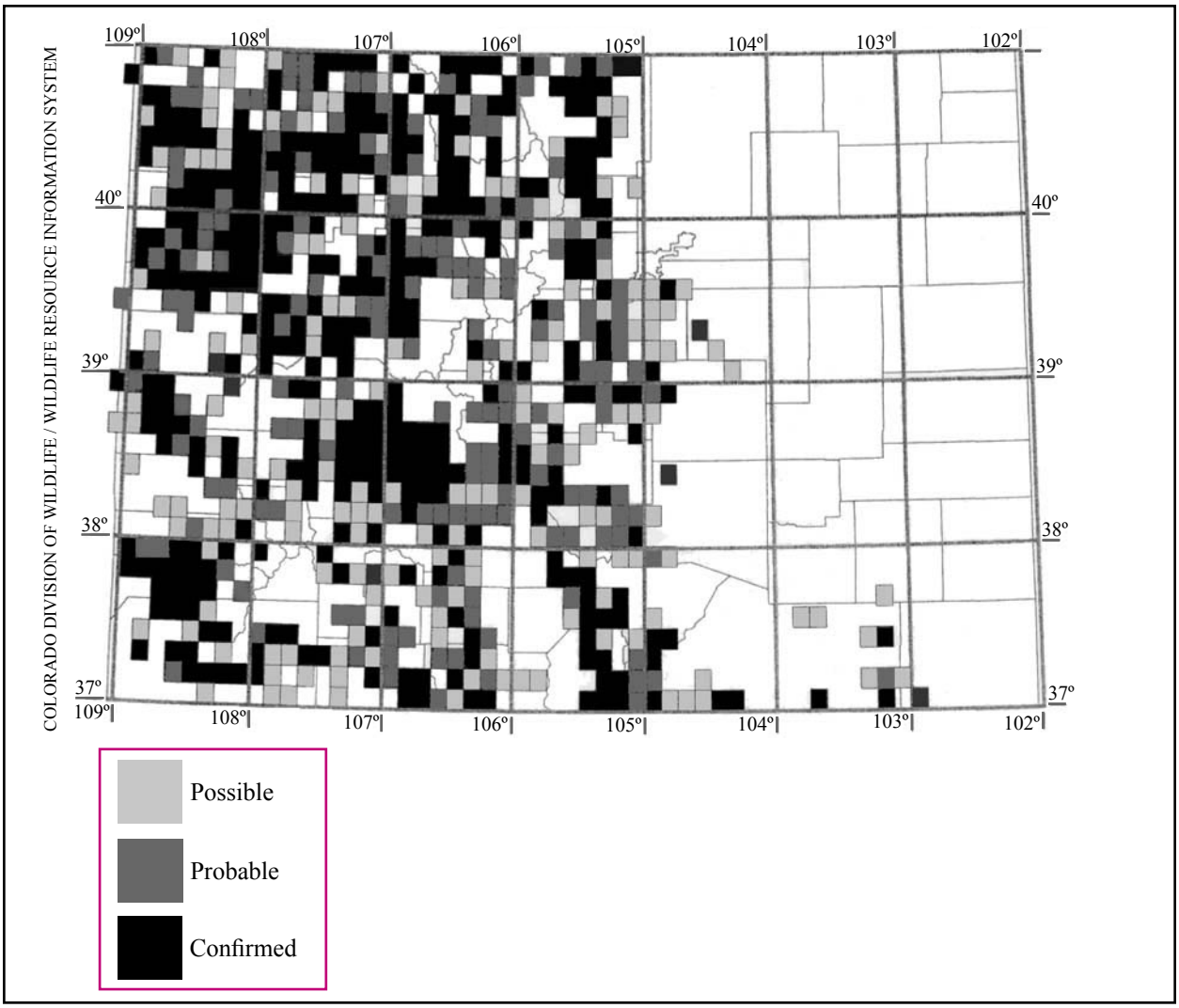

Figure 6. Breeding distribution of the green-tailed towhee in Colorado, based on extensive field work throughout the state from 1987 to 1994 (Righter 1998; map courtesy of the Colorado Bird Atlas Project).

the precision of BBS data affect the interpretation of population trends, and any conclusions deserve cautious treatment. Data from Wyoming, for instance, are deficient and not precise enough to detect even a 5 percent per year change (Sauer et al. 2004). Nevertheless, range-wide data and Colorado data are relatively robust. Although they show generally negative trends, none are statistically significant, and all confidence intervals overlap zero, indicating stable populations (**Table 1**; Sauer et al. 2004). Christmas Bird Count data likewise indicate stable winter populations (**Table 2**; Sauer et al. 1996).

Movements

A nocturnal, short- to medium-distance migrant, the green-tailed towhee is the only entirely migratory species in the genus *Pipilo* (Byers et al. 1995). Northbound spring migrants may begin departing wintering areas as early as late February, with small numbers lingering on wintering areas until mid-May. Spring migrants begin arriving in New Mexico and Arizona from mid-March to mid-April, but they typically begin arriving on their breeding grounds from late April to early May (e.g., northern Arizona, Utah, Oregon, Colorado, and Wyoming; summarized by Dobbs et al. 1998). An 11-year average arrival date at Laramie, Wyoming is 11 May (Norris 1968).

Throughout the breeding range, there is a noticeable upslope movement to subalpine meadows in July or August, presumably for molting and fat deposition in preparation for migration (Morton 1991; summarized by Dobbs et al. 1998). Southbound

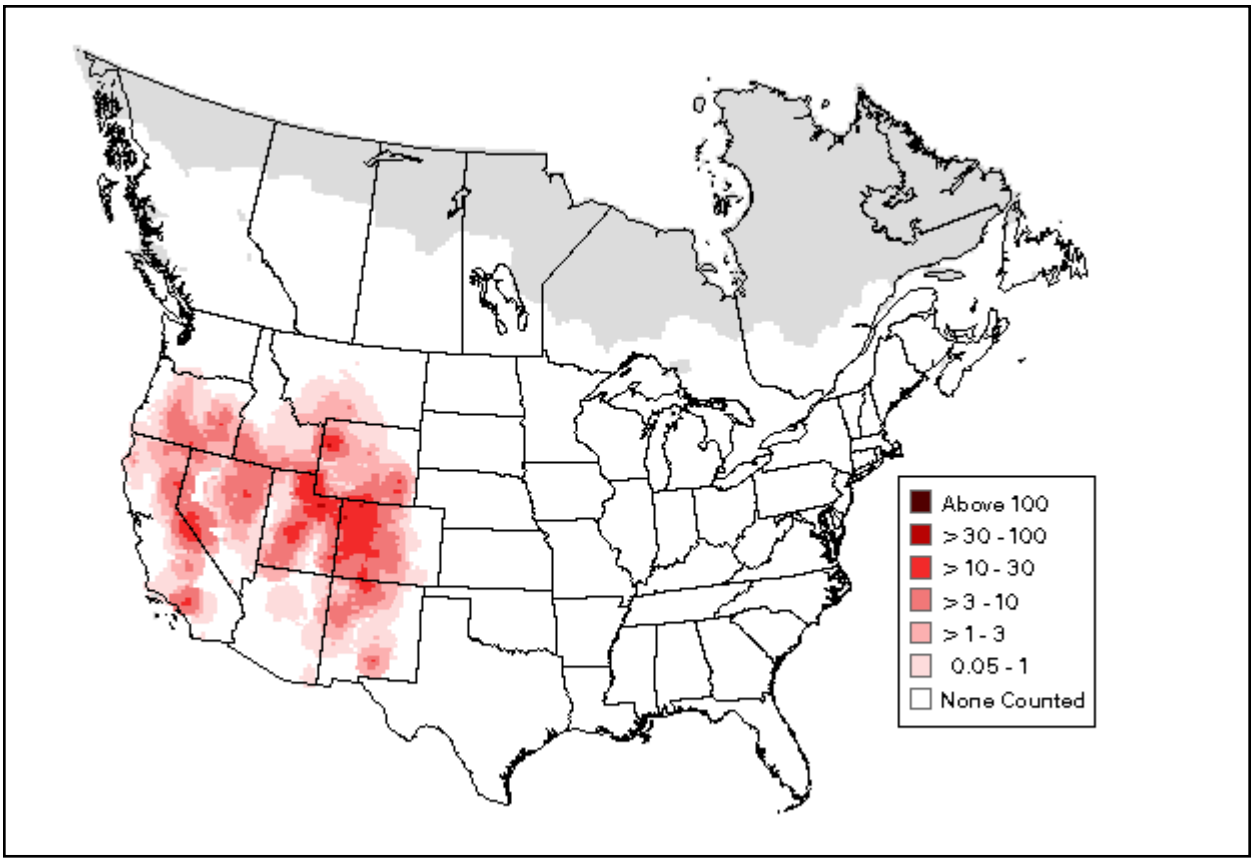

Figure 7. Relative abundance of breeding green-tailed towhees along Breeding Bird Survey routes, 1994-2003 (Sauer et al. 2004).

Table 1. Breeding Bird Survey results (1966-2003) for the green-tailed towhee in states and selected regions (Sauer et al. 2004). States within Region 2 are in bold print.

State / Region	Trend (percent change per year)	P	*N* (routes per year)	95% C. I.	Relative abundance (birds per route)
California	0.7	0.49	52	-1.3, 2.6	2.6
Colorado	**-1.0**	**0.33**	**80**	**-3.0, 1.0**	**9.7**
Idaho	-2.4	0.28	16	-6.7, 1.8	1.8
Montana‡	-2.3	0.37	8	-6.8, 2.3	0.2
Nevada†	-6.4	0.27	14	-17.3, 4.4	3.8
New Mexico	-0.4	0.73	21	-2.9, 2.1	2.2
Oregon	-1.1	0.34	35	-3.2, 1.1	1.7
Utah‡	4.5	0.00	35	1.7, 7.3	4.5
Wyoming‡	**-0.6**	**0.66**	**50**	**-3.3, 2.0**	**4.8**
Southern Rockies	-1.1	0.49	65	-4.1, 2.0	10.1
Wyoming Basin‡	0.6	0.81	31	-4.4, 5.7	2.5
Survey-wide	-0.4	0.43	312	-1.3, 0.6	3.19

† Data with a deficiency: low regional abundance (<1.0 birds per route), low sample size (<14 routes), or imprecise data (3 percent per year change not detectable).

‡ Data with an important deficiency: very low regional abundance (<0.1 birds per route), very low sample size (<5 routes), or very imprecise data (5 percent per year change not detectable).

Table 2. Christmas Bird Count data (1959-1988) for the green-tailed towhee (Sauer et al. 1996). (The species does not regularly winter in Region 2.)

Region	Trend (percent change per year)	*N* (count circles per year)	95% C. I.	Relative abundance (birds per 100 party hours)
Arizona	0.1	35	-2.0, 2.2	1.22
California	0.1	34	-0.8, 1.0	0.02
New Mexico	-0.7	21	-4.5, 3.0	0.23
Texas	-0.1	69	-1.6, 1.3	0.50
Survey-wide	0.0	197	-1.5, 1.4	0.28

migration begins from late July to mid-August and peaks from late August through September across much of the breeding range (e.g., Oregon, Colorado, Wyoming), extending into October in Arizona and New Mexico.

There are no known trends regarding migration routes; in fact, very little is known about green-tailed towhee natural history during migratory periods. The birds may travel in pairs or small, conspecific groups during migration, but males are often solitary during spring migration and begin acting territorial prior to arriving on the breeding grounds (Dotson 1971, Byers et al. 1995, Dobbs et al. 1998).

Habitat

Breeding habitat

Green-tailed towhees breed in a range of mixed-species shrub communities, including open shrubsteppe, montane shrubland, and successional growth in disturbed coniferous forest (Dobbs et al. 1998, Hutto and Young 1999). Montane shrubland is a heterogeneous habitat that occurs in patches of varying contexts, and may be confined to moist drainages, occur patchily in open woodlands, or comprise extensive areas on open slopes (Berry and Bock 1998). Green-tailed towhees prefer areas of high shrub species diversity in sagebrush (*Artemisia*)-dominated communities, in foothill shrublands, and within open pinyon (*Pinus*)-juniper (*Juniperus*) woodland (Wiens and Rotenberry 1981, Sedgwick 1987, Knopf et al. 1990, Berry and Bock 1998). In shrubsteppe environments throughout their range, green-tailed towhees prefer ecotones between big sagebrush (*A. tridentata*) and other shrub species, especially mountain mahogany (*Cercocarpus montanus*), but also chokecherry (*Prunus virginiana*), Utah juniper (*J. osteosperma*), snowberry (*Symphoricarpos*), and serviceberry (*Amelanchier*) (Knopf et al. 1990). In mid-elevation (ca. 2,600 m) mixed-conifer and ponderosa pine (*Pinus ponderosa*) forest in Arizona, green-tailed towhees breed in shrubby regrowth resulting from fire or logging, characterized by patches of small white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), New Mexico locust (*Robinia neomexicana*), Gambel oak (*Quercus gambelii*), raspberry (*Rubus*), and gooseberry (*Ribes*) (Dobbs et al. 1998).

In Region 2, breeding habitat is well-documented in Colorado, where green-tailed towhees occur primarily in montane shrubland, in which the most common shrubs are snowberry, serviceberry, chokecherry, bitterbrush (*Purshia tridentata*), mountain mahogany, squaw apple (*Peraphyllum ramosissimum*), Gambel oak, and sagebrush (Berry and Bock 1998, Righter 1998, Leukering et al. 2004). In Colorado, green-tailed towhees also breed in sagebrush shrubland (shrubsteppe), semi-desert shrubland, montane riparian shrubland, and where conditions are appropriate within pinyon-juniper and ponderosa pine woodland, and aspen and mixed-conifer forest (Righter 1998, Leukering et al. 2004, Beason et al. 2005). In northwestern Colorado, for example, green-tailed towhees are common in sagebrush-dominated open areas within pinyon-juniper woodland (Sedgwick 1987). In foothill shrubland in the Colorado Front Range, common shrub species include skunkbrush (*Rhus aromatica*), mountain mahogany, chokecherry, wild plum (*Prunus americana*), and hawthorn (*Crataegus*) (Berry and Bock 1998). Montane shrubland-woodland savanna, at ecotones of or within very open areas of ponderosa pine woodland, also represents an important habitat for green-tailed towhees in the Front Range. This habitat consists of sagebrush, bitterbrush, common juniper (*Juniperus communis*), and rabbitbrush (*Chrysothamnus viscidiflorus*) shrubs, among others, and scattered (canopy cover <25 percent) mature ponderosa pine trees (**Figure 8**; Jehle 2004).

Green-tailed towhee habitat relationships are less well known in Wyoming. Throughout that state, however, the green-tailed towhee is most common in shrubsteppe habitat and in habitats that include

Figure 8. Green-tailed towhee breeding habitat: montane shrubland with elements of shrub-pine savanna, Rocky Mountain National Park, Larimer County, Colorado (photograph by R.C. Dobbs, July 2005).

a significant shrubsteppe component (e.g., juniper woodland) (**Table 3**; Faulkner 2005). In southwestern Wyoming, the species breeds in open Utah juniper woodland with an understory dominated by big sagebrush, mountain mahogany, rabbitbrush, and bitterbrush (Pavlacky and Anderson 2004). In that habitat, green-tailed towhees prefer areas with greater tree height and grass cover, moderate overstory and shrub cover, and lower seedling/sapling cover than other breeding birds (Pavlacky and Anderson 2004). In the Bighorn and Shoshone national forests, relative abundance is much higher in shrubsteppe and montane grassland, which includes shrubsteppe, than other habitats sampled (i.e., montane riparian, low-, mid-, and high-elevation conifer forests) (**Table 3**; Faulkner 2005).

Microhabitat characteristics

In shrubsteppe communities, the vigor of shrub patches (i.e., percentage of live branches, herbaceous biomass) is the best descriptor of green-tailed towhee microhabitat, presumably due to increased concealment for nests or foraging birds, or increased food availability (Knopf et al. 1990). Similarly, in montane shrubland near ponderosa pine ecotones in Colorado, green-tailed towhee nest sites have greater live-shrub cover, as well as greater shrub cover in general, than randomly-selected sites (Jehle 2004). In both shrubsteppe and montane shrubland, the species prefers heterogeneous areas characterized by high local shrub species diversity (Knopf et al. 1990, Berry and Bock 1998). In open areas of coniferous forest in Arizona, green-tailed towhee nest sites tend to be located at the dry end of a moisture gradient and, within a 5-m radius nest-centered patch, have more small locusts, oaks, and firs, but fewer canyon maples (*Acer grandidentatum*), and more ground cover than at random sites or at nest sites of coexisting shrub-nesting species (Martin 1998).

Non-breeding habitat

Green-tailed towhees use a wide variety of habitats during migration, including montane areas, riparian woodlands, and upland desert, but they tend to use brushy areas at lower elevations (Dobbs et al. 1998). In Colorado, transients occur in montane valleys and foothills within the breeding range, as well as in wooded or brushy riparian areas at the base of the foothills and onto the eastern plains, including

Table 3. Relative abundance of green-tailed towhees breeding in different areas and habitats in Wyoming (data from Faulkner 2005).

	Number of birds[1]	Number of transects[2]
Statewide		
Shrubsteppe	1.7 ± 0.7	28.3
Juniper woodland[3]	5.1 ± 1.6	23.3
Montane riparian	1.7 ± 0.8	20.3
Mid-elevation conifer forest	1.0 ± 0.7	23.7
Aspen	2.0 ± 0.7	24.7
Shortgrass prairie	0.4 ± 0.2	23.3
Bighorn National Forest		
Shrubsteppe	5.9 ± 2.1	10
Montane riparian	0.3 ± 0.3	12
Low-elevation conifer forest	0.2 ± 0.2	10
High-elevation conifer forest	0.1 ± 0.1	10
Shoshone National Forest		
Montane grassland[4]	2.7 ± 0.4	9.7
Montane riparian	1.4 ± 0.6	8.7
Mid-elevation conifer forest	0.2 ± 0.2	8.3

[1]Mean ± SD number of green-tailed towhees per 15-point transect, over three years.
[2]Mean number of 15-point transects per year.
[3]This habitat often includes a strong shrubsteppe component (Faulkner 2005).
[4]This habitat consists of typical grassland and shrubsteppe components (Faulkner 2005).

urban areas (Andrews and Righter 1992). In Arizona, green-tailed towhees use low-elevation desert washes as migratory stopover habitat more often than upland desert or high-elevation desert washes (Szaro and Jakle 1985). On western Texas and southern Arizona wintering grounds, green-tailed towhees primarily occur in arid desert habitats characterized by acacia (*Acacia* spp.), honey mesquite (*Prosopis glandulosa*), and creosote bush (*Larrea tridentata*), and along mesquite-lined washes in desert grassland (Dobbs et al. 1998; R. C. Dobbs personal observation).

Food habits and foraging ecology

Green-tailed towhees forage on the ground and low in shrubby vegetation, typically beneath or within dense overhead or surrounding vegetation or brush, or at the edge of thick cover during the breeding and nonbreeding seasons (Dobbs et al. 1998). They eat primarily seeds and small insects that they typically find on the ground through bilateral scratching (Dobbs et al. 1998). Using this technique, a bird hops forward and then simultaneously kicks both feet backwards, moving leaf litter and duff and exposing lower layers or bare ground. With its bill pointed downward, the bird locates exposed food visually and attacks food items with its bill. Green-tailed towhees also glean insects from foliage in low branches of shrubs and small trees during the breeding season (Dobbs et al. 1998).

In addition to grass and weed seeds (e.g., pigweed [*Amaranthus*], filaree [*Erodium*], dandelion [*Taraxacum*], ricegrass [*Oryzopsis*]; Oberholser 1974), green-tailed towhees eat beetles (Coleoptera); bees and wasps (Hymenoptera); butterflies, moths, and their larvae (Lepidoptera); grasshoppers and crickets (Orthoptera); true bugs (Hemiptera); and flies (Diptera) (Norris 1968, Dotson 1971). During the breeding season in California, in post-fire shrubby regrowth in the Sierra Nevada, green-tailed towhees ate 72 percent seeds and 28 percent insects (n = 28 stomachs; Beaver 1976).

Breeding biology

Phenology

Pair formation occurs when the female arrives on the breeding grounds, which occurs within one week of male arrival (Dotson 1971), typically mid-May but extending through mid-June in northern Arizona (Dobbs et al. 1998). The female builds the nest in two to five days, without male assistance. Most females

lay first eggs of first clutches 28 May (mode date) in northern Arizona (range 4 May-9 June, n = 76; Dobbs et al. 1998). Average completion date of first clutches in Grand County, Colorado is 5 June (n = 56; B. P. Gibbons, T. Leukering, and S. W. Hutchings, unpublished data). Throughout their range, green-tailed towhees typically have eggs from late May to mid-July and nestlings from mid-June to late July (**Table 4**). In Region 2, data from Colorado show eggs from 24 May to 23 July, nestlings from 7 June to 27 July, and fledglings from 2 June to 22 August (**Table 4**). Nesting phenology does not appear to differ between sagebrush shrubsteppe and montane shrubland in northern Colorado (**Table 5**). Females typically attempt to renest following nest failure, as late as July in northern Arizona (Dobbs et al. 1998), and may produce two clutches per year in some areas (e.g., northern Colorado; B. P. Gibbons personal communication, November 2004.

Nests

Green-tailed towhee nests are bulky, thick-walled, deep cup-shaped nests (**Figure 9**) composed of twigs, stems, and grasses, and lined with fine stems, rootlets, and hairs (Norris 1968, Dobbs et al. 1998). Nests are located from the ground (at the base of shrubs or bunchgrasses) up to about 75 cm in shrubs and small trees. Average nest height in well-studied populations ranges from 33 cm in montane shrubland in Colorado (Jehle 2004) to 63 cm in disturbed mixed-conifer forest in northern Arizona (Dobbs et al. 1998). Nests are typically very well-concealed by vegetation of the substrate or adjacent grasses, shrubs, or small trees. From above, nest concealment averages 90.1 percent at a northern Colorado site (Jehle 2004).

Use of plant species as nest substrates varies with geographic location and habitat composition (Tables 6, 7). Green-tailed towhees often nest in saplings of canopy tree species (e.g., white fir) in post-disturbance, early-successional sites within mixed-conifer forest (**Table 6**; Dobbs et al. 1998). In shrub-dominated communities, green-tailed towhees build nests in a wide variety of shrub species, often sagebrush, bitterbrush, or snowberry. This pattern is true in Region 2, where Colorado data from throughout the state show that green-tailed towhees use sagebrush, bitterbrush, and snowberry relatively frequently (**Table 7**; B. P. Gibbons, T. Leukering, and S. W. Hutchings unpublished data; Jehle 2004). In Rocky Mountain

Table 4. Nesting phenology of the green-tailed towhee. State within Region 2 is in bold print. Sample sizes (n) refer to numbers of nests.

State	Building	Eggs	Nestlings	Fledglings
Colorado[1]	**3 May-6 Jul**	**24 May-23 Jul**	**4 Jun-30 Jul**	**2 Jun-22 Aug**
New Mexico[2]		20 May-18 Jul	15 Jun-25 Jul	
Arizona[3]	mid-late May	4 May-23 Jul	16 May-early Aug	
Utah[4]	25 May-25 Jun	27 May-15 Jul	14 Jun-29 Jul	
Oregon[5]		28 May-5 Jul	20 May-12 Jul	late Jun-Aug

[1]Colorado (Building n = 38, Eggs n = 276, Nestlings n = 230, Fledglings n = 288); Bailey and Niedrach 1965; Righter 1998; Jehle 2004; G. Jehle unpublished data; CNRCP unpublished data; B.P. Gibbons, T. Leukering, and S.W. Hutchings unpublished data

[2]New Mexico (Eggs n >16; Nestlings n = 13); Bailey 1928; CNRCP unpublished data

[3]Arizona; Dobbs et al. 1998

[4]Utah (Building n = 3, Eggs n = 8, Nestlings n = 8); Dotson 1971; CNRCP unpublished data

[5]Oregon (Nestlings n = 21, Fledglings n = 15); Scheuring and Powell 2003; CNRCP unpublished data

Table 5. Nesting phenology of the green-tailed towhee in different habitats in Colorado. Sample sizes (n) refer to numbers of nests.

Habitat, County	Building	Eggs	Nestlings
Sagebrush shrubland, Grand[1]	6 Jun-9 Jun	29 May-13 Jul	4 Jun-25 Jul
Ponderosa pine-shrub, Larimer[2]	31 May-27 Jun	31 May-21 Jul	12 Jun-30 Jul

[1]Data collected May-August 1996-1997, at 2400 to 2600 m elevation near Kremmling, CO (Building n = 1, Eggs n = 59, Nestlings n = 64); B. P. Gibbons, T. Leukering, and S. W. Hutchings unpublished data

[2]Data collected May-August 2002-2003, at 2360 to 2900 m elevation in Rocky Mountain National Park (Building n = 25, Eggs n = 152, Nestlings n = 146); Jehle 2004; G. Jehle unpublished data

Figure 9. Green-tailed towhee nest with eggs, Rocky Mountain National Park, Larimer County, Colorado (photograph by R.C. Dobbs, June 2005).

Table 6. Percent use of plant genera as nest substrates by green-tailed towhees at study sites outside of Region 2.

Nest Substrate	Arizona[1]	New Mexico[2]	Oregon[3]	Utah[4]
Abies	82.8			
Acer	2.3			
Artemisia			42.1	100.0
Chrysothamnus			5.3	
Lupinus			5.3	
Pseudotsuga	3.9	12.5		
Purshia			10.5	
Ribes	1.6			
Robinia	7.0			
Symphoricarpos		87.5	10.5	
Other spp. (incl. *Rubus*)	2.4			
Bunchgrass spp.			26.3	

[1]Mogollon Rim, Coconino Co., AZ; habitat: early successional regrowth within mixed-conifer (pine-fir-aspen) forest, ca. 2600 m elevation (n = 129; Dobbs et al. 1998)

[2]Northeast of Albuquerque, Bernalillo Co., NM; habitat: mixed (pine-fir-aspen) woodland, ca. 2100 m elevation (n = 16; CNRCP unpublished data)

[3]Hart Mountain National Antelope Range, Lake Co., OR; habitat: shrubsteppe, ca. 1400 m elevation (n = 19; CNRCP unpublished data)

[4]Mountain Dell Canyon, Salt Lake Co., UT; habitat: shrubsteppe, ca. 1800 m elevation (n = 10; Dotson 1971)

Table 7. Percent use of plant genera as nest substrates by green-tailed towhees in Colorado.

Nest Substrate	Statewide[1]	Grand Co.[2]	Larimer Co.[3]
Acer (maple)	2.9		1.1
Amelanchier (serviceberry)	5.9	2.5	
Artemisia (sagebrush)	32.4	57.0	35.9
Artemisia-Purshia		6.3	
Artemisia-Symphoricarpos		3.8	
Chrysothamnus (rabbitbrush)		1.3	
Jamesia (hydrangia)			0.5
Juniperus (juniper)			51.6
Picea (spruce)	2.9		
Prunus (chokecherry)	2.9		
Pseudotsuga (Douglas-fir)			0.5
Purshia (bitterbrush)	2.9	26.6	8.2
Quercus (oak)	8.8		
Rhus (sumac)	5.9		
Ribes (gooseberry, currant)			2.2
Salix (willow)	5.9		
Symphoricarpos (snowberry)	17.6	2.5	
Unknown shrub	8.8		
Stipa (bunchgrass)	2.9		

[1] n = 34; various habitats (Righter 1998; CNRCP unpublished data)
[2] n = 79; sagebrush shrubland habitat (B.P. Gibbons, T. Leukering, and S.W. Hutchings unpublished data)
[3] n = 184; montane shrubland habitat (Jehle 2004)

National Park, Colorado, green-tailed towhees nested in common juniper in greater proportion to its availability (Jehle 2004).

Breeding behavior

Courtship: Courtship behavior involves intra-pair interactions and displays, in which a male may display to a female or vice-versa. A male typically displays to a female by holding nesting material in his bill, bowing forward while pointing his bill and tail upward, and quivering his wings (Dobbs et al. 1998). Such displays often precede copulation, which occurs on or near the ground beneath vegetative cover and lasts 1 to 3 seconds (Dotson 1971, Dobbs et al. 1998). Other pre-copulatory interactions appear hostile, such as when a male and a female face each other and aggressively and physically interact. Males often follow females closely during the fertile period, immediately preceding and during egg-laying.

Nest-building: Females build nests over a two to five day period (Dobbs et al. 1998). Periods of active nest building, with frequent trips to the nest, are interspersed with periods of no building. Males sing and call in the vicinity of actively building females, and while they will visit the nest during building, they are not known to directly assist in building the nest (Dobbs et al. 1998).

Eggs and egg-laying: Green-tailed towhee eggs have a pale, turquoise-tinted ground color and reddish brown speckling, which usually is concentrated on the larger end (**Figure 9**). Across the species' range, egg measurements average 21.85 mm in length (range 18.51 to 25.40 mm) by 16.37 mm in breadth (range 15.14 to 17.70 mm) (n = 91 eggs [23 clutches] in Western Foundation of Vertebrate Zoology collection; Dobbs et al. 1998). Female green-tailed towhees lay a single egg per day, usually in the early morning; they lay eggs on consecutive days until the clutch is complete and rarely skip a day.

Incubation: Incubation usually begins the morning that the penultimate egg is laid. Only the female green-tailed towhee incubates (only the female has a brood patch), but the male occasionally feeds his mate at the nest as she incubates. In Arizona, females spend about 70 percent of their time incubating during morning hours, in which bouts on the nest average 28.6

minutes (range 1 to 80 minutes) and bouts away from the nest average 12.4 minutes (range 5 to 31 minutes) (Dobbs et al. 1998). The incubation period lasts an average of 12 days in Larimer County, Colorado (n = 45; Jehle 2004) and 12.75 days in Grand County, Colorado (range 12 to 13 days, n = 8; B. P. Gibbons, T. Leukering, and S. W. Hutchings unpublished data), both of which are similar to the 12-day averages documented in northern Arizona (range 11 to 13 days; Dobbs et al. 1998) and northern Utah (range 11 to 13 days; Dotson 1971). Among nests that survive to the nestling stage in Colorado, 95.03 percent of eggs hatch (n = 48 nests; Cornell Nest Record Card Program unpublished data). Most eggs in a clutch hatch on the same day, usually before noon, but they may hatch as much as one day apart (Dobbs et al. 1998).

Parental care: Only female green-tailed towhees brood nestlings (**Figure 10**), spending 70 to 80 percent of their time on nests during the first two days following hatching, but less time thereafter (Dotson 1971, Dobbs et al. 1998). Male and female parents feed nestlings and dispose of nestlings' fecal sacs, either by eating them at the nest or carrying them away from the nest for disposal (Dotson 1971). The nestling period lasts an average of 10 days in Larimer County, Colorado (n = 77; Jehle 2004) and 9.6 days in Grand County, Colorado (range 8 to 13 days, n = 35; B. P. Gibbons, T. Leukering, and S. W. Hutchings unpublished data), both of which are similar to that documented in northern Utah (Dotson 1971), but notably less than the 11 to 14 day nestling period in northern Arizona (Dobbs et al. 1998). Adults feed fledglings for at least 2 weeks after they leave the nest.

Nest parasitism

The green-tailed towhee is an occasional host of the brown-headed cowbird (*Molothrus ater*) (Friedmann and Kiff 1985), but the frequency of nest parasitism may vary with land use and cowbird abundance. The green-tailed towhee enjoys zero brood parasitism where well studied in Region 2, including montane shrubland in Larimer County, Colorado (n = 186 nests; G. Jehle personal communication, October 2004) and shrubsteppe in Grand County, Colorado (n = 79 nests;

Figure 10. Green-tailed towhee nest with four nestlings, 5 to 6 days old, Rocky Mountain National Park, Larimer County, Colorado (photograph by G. Jehle, July 2003).

B. P. Gibbons, T. Leukering, and S. W. Hutchings unpublished data), and elsewhere (e.g., northern Arizona; Dobbs et al. 1998). Anecdotal accounts, however, suggest that parasitism pressure may be high in places (e.g., Mesa County, Colorado; Chace and Cruz 1996). Nevertheless, extensive breeding bird atlas field work throughout Colorado from 1987 to 1994 revealed only four instances of cowbird parasitism among 320 green-tailed towhee post-nest building breeding records (Chace and Cruz 1996, Righter 1998). Of 77 other post-nest building breeding records, from Region 2 (n = 23) and elsewhere (n = 54), only one indicates evidence of cowbird parasitism (Cornell Nest Record Card Program unpublished data).

Demography

Population size and density

The range-wide population estimate for the green-tailed towhee is 4,100,000 individuals (Rich et al. 2004). Within Region 2, Righter (1998) estimated that approximately one million pairs breed in Colorado alone. Regardless of the reliability of these estimates, Colorado contains a significant portion of the entire green-tailed towhee population. In addition to northern Utah, California's Sierra Nevada, and areas of western Wyoming and southern California, BBS data show the highest regional abundance of green-tailed towhees in western Colorado (**Figure 7**), further illustrating the importance of Region 2 to the overall breeding population.

Within Region 2, breeding density varies strongly among habitat-types, ranging in Colorado from 0.025 birds per ha (2-year average) in semi-desert shrubland to 1.051 birds per ha (4-year average) in montane shrubland (**Figure 11**). The average breeding density of 0.15 birds per ha (3 pairs per 40 ha) reported from aspen and aspen-spruce habitats in Colorado (Winternitz 1976) generally is similar to that found by the Monitoring Colorado's Birds (MCB) program

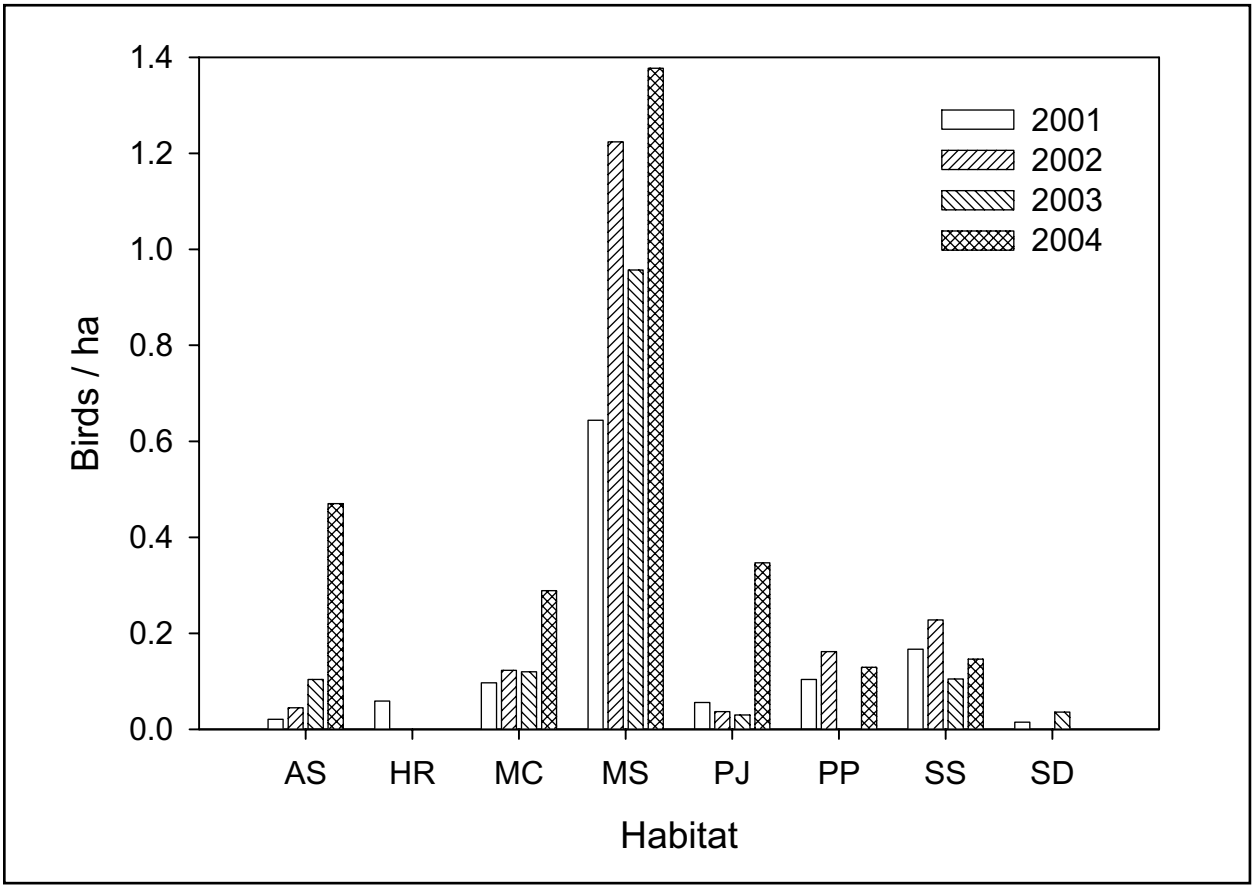

Figure 11. Breeding densities of green-tailed towhees in Colorado, in aspen (AS), high-elevation riparian (HR), mixed-conifer (MC), montane shrubland (MS), pinyon-juniper (PJ), ponderosa pine (PP), sage shrubland (SS), and semi-desert shrubland (SD) habitats (data from Leukering and Levad 2003, Leukering et al. 2002, 2004, Beason et al. 2005).

in similar habitats, given annual variation (**Figure 11**). In addition to annual variation within habitat types, breeding density varies with shrub cover and/or management practices (i.e., prescribed burning). In northern Colorado montane shrubland, green-tailed towhee breeding density is highest (1.97 birds per ha) on unburned sites with high (35 percent) shrub cover, and lowest (0.05 birds per ha) on recently burned sites with low (5 percent) shrub cover (Jehle 2004).

Reported estimates of territory size range from 3.7 ha per pair in aspen habitat in southeastern Oregon (Maser et al. 1984) to 0.09 ha per pair in northern Utah shrubsteppe (Dotson 1971); methods used to determine territory size were not reported. Variation in territory size may reflect geographic variation in population density. That is, individual pairs may be able to maintain larger territories in southeastern Oregon, where population density is relatively low, than in northern Utah, where population density is relatively high (**Figure 7**).

Age of first reproduction

Age of first breeding attempt has not been documented; however, like other emberizids, females almost certainly breed during their second year (i.e., when one year old) and annually thereafter.

Clutch size and annual reproductive success

Average (± SE) clutch size is 3.57 ± 0.057 eggs in early successional areas within mixed-conifer forest in northern Arizona (range 2 to 5, n = 126; BBIRD 2004; see also Dobbs et al. 1998). In northern Colorado, clutch size averages 3.77 ± 0.085 eggs in shrubsteppe (range 2 to 5, n = 52; Cornell Nest Record Card Program unpublished data) and 3.70 eggs in montane shrubland (range 2 to 5, n = 152; Jehle 2004).

Annual reproductive success appears to vary among habitats. In Colorado, estimates of nest success range from 46.5 percent in shrubsteppe (B. P. Gibbons, T. Leukering, and S. W. Hutchings unpublished data) to 57 percent in montane shrubland (Jehle 2004) (**Table 8**). In early successional areas of mixed-conifer forest in northern Arizona, nest success is only 24.3 percent (**Table 8**; BBIRD 2004). The primary cause of nest failure is predation of eggs and nestlings, both in Colorado (83 percent of nest failures; B. P. Gibbons, T. Leukering, and S. W. Hutchings unpublished data) and in Arizona (75 percent of nest failures; Dobbs et al. 1998). Other causes of nest failure include predation of adults, severe weather (e.g., hail), and human activity (Huey 1936, Dobbs et al. 1998, Cornell Nest Record Card Program unpublished data).

The number of broods produced per year appears to vary with habitat, possibly mediated by nest predation pressure. In Arizona, where nest success is low, green-tailed towhees are very rarely, if ever, double-brooded (Dobbs et al. 1998). In Grand County, Colorado, however, where nest success is relatively high, the species is regularly double-brooded, which was documented with color-banded adults (B. P. Gibbons, T. Leukering, and S. W. Hutchings unpublished data).

Table 8. Summary of green-tailed towhee breeding productivity at well-studied sites. Clutch sizes are mean ± SE, with ranges in parentheses. Daily survival rates (DSR) were calculated using exposure (Mayfield) methods. Overall nest survival is the likelihood of a clutch surviving to fledge at least one young bird.

	Grand Co., CO[1]	Larimer Co., CO[2]	Coconino Co., AZ[3]
Clutch Size	3.76 ± 0.085 (2-5)	3.70 (2-5)	3.57 ± 0.057 (2-5)
Nesting Success			
Egg-laying DSR	—	—	0.924
Incubation DSR	0.969	0.978	0.937
Nestling DSR	0.963	0.970	0.961
Overall Nest Survival	46.5%	57.0%	24.3%

[1]Shrubsteppe habitat. Clutch size: n = 52 nests (CNRCP, unpublished data); nesting success: DSR based on 872 exposure days; overall nest survival calculated using a 12.75-day incubation period and a 9.6-day nestling period (B.P. Gibbons, T. Leukering, and S.W. Hutchings, unpublished data).

[2]Montane shrubland habitat. Clutch size: n = 152 nests (Jehle 2004); overall nest survival calculated assuming 12-day incubation and 10-day nestling periods (n = 179 nests; Jehle 2004).

[3]Early successional habitat in disturbed areas of mixed-conifer forest. Clutch size: n = 126 (BBIRD 2004); Nesting success: DSR based on 1849.5 exposure days (n = 170 nests); overall nest survival calculated assuming 3-day egg-laying, 12-day incubation, and 10-day nestling periods (BBIRD 2004; see also Martin and Li 1992, Dobbs et al. 1998).

Annual survival

Estimates of annual survival probability of adult green-tailed towhees are based on capture-recapture data among years from banding sites in Oregon. Mean (± SE) annual survival probability is 0.56 ± 0.14 (n = 13 [males only]; King and Mewaldt 1987) and 0.512 ± 0.12 (n = 15; Institute for Bird Populations 2003). Survival probability of young birds, from their first fall to their second year, has not been quantified. The maximum age recorded for a banded bird is 7.67 years (Klimkiewicz and Futcher 1987). Predation is likely a major cause of mortality for adult birds (see Community ecology section); other documented causes of adult mortality include severe weather (Whitmore et al. 1977) and collisions with automobiles (H.A. Green in Dobbs et al. 1998).

Breeding site fidelity

Return rates indicate that fidelity to breeding sites is similar to that of most passerines (King and Mewaldt 1987). In Colorado, five of 16 banded males returned to the same territory the following year (P.S. Kaplan in Dobbs et al. 1998), and in northern New Mexico, three of six banded adults returned to the same breeding area the following year (Zwartjes and Farley 1998).

Dispersal patterns

Little information is available on green-tailed towhee dispersal ecology; banded birds have not been recovered away from original banding sites. Natal dispersal patterns between birth sites and first breeding sites have not been documented, although post-fledging dispersal has been described for juveniles prior to fall migration. In the Sierra Nevada, California, juveniles move upslope from birth sites to subalpine meadows, presumably due to greater food resources in more mesic subalpine areas and their need to acquire fat prior to fall migration (Morton 1991). This phenomenon appears to be widespread, with similar late summer upslope movements described in many areas of the species' range, including Colorado (Packard 1946).

Matrix model analysis

Demographic modeling is an important tool that allows conservationists to predict if a population is likely increasing, decreasing, or remaining stable, and to identify the demographic parameters that may be most important in limiting population growth (McDonald and Caswell 1993, Caswell 2001). I used a matrix model to estimate the population growth rate (λ), and sensitivity and elasticity analyses to examine the relative importance of different demographic parameters to λ. While this approach produces valuable information on green-tailed towhee demography, readers should interpret results with caution due to limitations of the data and assumptions of the model (see below).

I constructed a life-cycle diagram for the green-tailed towhee consisting of two stages (juvenile and adult) and transitions between stages (**Figure 12**; McDonald and Caswell 1993, Caswell 2001). Based on this life cycle, I developed a two-stage matrix population model, illustrated as:

$$\begin{matrix} F_1 & F_2 \\ P_1 & P_2 \end{matrix}$$

In this model, F_i represents fecundity in stage i and is calculated by $F_i = (P_i)(m_i)$, where m_i is the average number of female offspring produced per female in stage i, and P_i is annual survival in stage i. I calculated fecundity by m_i = (3.75)(1)(0.5)(0.95)(0.57) = 1.02, using data from Region 2 where possible. Values used in the fecundity equation are as follows: 3.75 is an estimate of clutch size in Region 2 (see Clutch size and annual reproductive success, above), 1 is an estimate of the number of broods produced per female per year (Dobbs et al. 1998; but see Breeding Biology, above), 0.5 refers to female offspring, assuming a 1:1 sex ratio (because the model assumes female dominance, fecundity is portrayed as the number of female offspring per female), 0.95 is an estimate of the egg hatching rate in Region 2 (Cornell Nest Record Card Program unpublished data), and 0.57 is the best estimate of nest success available for Region 2 (Jehle 2004). Based on a lack of age-specific data, I assumed that fecundity does not vary with age in green-tailed towhees. Because no empirical data are available on the survival of juveniles to age 1 year, I assumed a stable population and estimated P_1 indirectly based on other parameter estimates (Noon and Sauer 1992, McDonald and Caswell 1993). I estimated adult survival (P_2) based on available empirical data (published estimates of 0.512 and 0.560; see Annual survival, above). These data produced the following numeric values for the matrix:

$$\begin{matrix} 0.464 & 0.546 \\ 0.455 & 0.536 \end{matrix}$$

Based on these vital rates, the matrix population analysis estimated population growth rate, λ = 0.999.

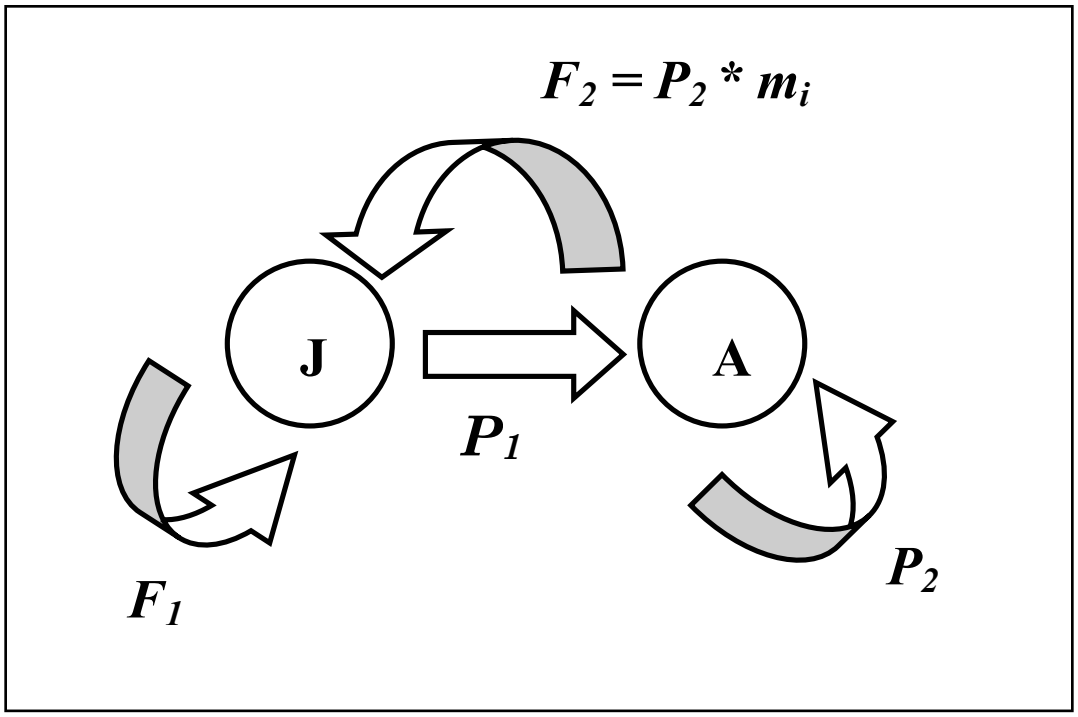

Figure 12. Life cycle diagram for the green-tailed towhee, consisting of two stages represented by nodes **J** (juvenile stage) and **A** (adult stage). Arrows represent survival and fecundity rates for juvenile and adult stages (F_1 and F_2 are fecundity rates of juveniles and adults, respectively; P_1 is the survival rate of juveniles to adulthood, and P_2 is annual adult survival).

Thus, this analysis suggests that green-tailed towhee populations are intrinsically stable or very close to stable.

Sensitivity and elasticity analyses allow us to examine how variation in vital rates affects λ. Sensitivity is the effect on population growth of absolute changes in vital rates, and it indicates the relative importance of a given vital rate to population growth. Sensitivities are thus useful in evaluating the relative importance of survival and reproductive transitions, which may provide insight into the most important focus for conservation. Land managers, for example, could use sensitivity analysis to determine which stage or demographic parameter is most important to increasing the population growth of a declining species. Sensitivity analysis is also useful because it allows evaluation of effects of inaccurate estimation of vital rates from field data, or from environmental perturbations (Caswell 2001). Sensitivity analysis of the matrix model that I constructed above, produced the sensitivity matrix:

0.463	0.455
0.546	0.536

The analysis suggests that λ is most sensitive to juvenile and adult survival. Hence, juvenile and adult survival are likely the most important demographic factors to population viability, if changes in vital rates are absolute as assumed by sensitivity analysis. Changes in vital rates, however, may not be absolute because different types of vital rates (i.e., survivorship and fecundity) are measured in different units, which are not necessarily comparable on the same scale.

Elasticity analysis avoids the problem of scale inherent to sensitivity analysis (see above) by examining the "sensitivity" (i.e., elasticity) of λ to proportional changes, rather than absolute changes, in vital rates. Because they reflect proportional changes, elasticities sum to 1.0. Like sensitivity analysis, elasticity analysis is useful because it allows managers to evaluate the relative importance of different stages and demographic parameters in determining the most important focus of conservation efforts. Elasticity analysis of the matrix model that I constructed above, produced the elasticity matrix:

0.215	0.248
0.248	0.287

The analysis suggests that λ is most elastic to changes in adult survival, which accounted for 28.7 percent of the total elasticity. Next most elastic were juvenile survival and adult reproduction, each of which accounted for 24.8 percent of total elasticity. These results suggest that variation in adult survivorship would likely have stronger effects on λ than other demographic parameters.

Community ecology

Ecological relationships of the green-tailed towhee are illustrated in an envirogram (**Figure 13**). The envirogram depicts the relationships among ecological factors that may affect the survival or reproductive success of individual birds. Factors are categorized as "centrum" factors, which may directly affect a bird's survival or reproductive success (e.g., food), and "web" factors, which may indirectly affect a bird's survival or reproductive success (e.g., habitat heterogeneity).

Predators

Predators of adult and juvenile green-tailed towhees include Cooper's hawk (*Accipiter cooperii*), peregrine falcon (*Falco peregrinus*), American kestrel (*F. sparverius*), red-tailed hawk (*Buteo jamaicensis*), and long-eared owl (*Asio otus*) (Dotson 1971), and likely sharp-shinned hawk (*Accipiter striatus*) and northern goshawk (*A. gentilis*). Steller's jay (*Cyanocitta stelleri*), red squirrel (*Tamiasciurus hudsonicus*), least chipmunk (*Tamias minimus*), and long-tailed weasel (*Mustela frenata*) are the primary predators of eggs and nestlings in high-elevation mixed-conifer forest in northern Arizona (Dobbs et al. 1998). In northern Utah shrubsteppe, black-billed magpie (*Pica pica*), striped skunk (*Mephitis mephitis*), spotted skunk (*Spilogale putorius*), and gopher snake (*Pituophis catenifer*) are thought to be important green-tailed towhee nest predators (Dotson 1971). In northern Colorado shrubsteppe, a garter snake (*Thamnophis* sp.) was observed depredating a green-tailed towhee nest, as well as a brewer's sparrow (*Spizella breweri*) nest. Garter snakes are suspected of being a major predator of green-tailed towhee nests (B. P. Gibbons personal communication, November 2004).

Adult towhees evade attacking predators by seeking shelter in cover of woody vegetation (Oberholser 1974). When on the nest, a female often attempts to lead an approaching predator away from the area with a characteristic "rodent run," in which she drops from the nest to the ground and runs, with tail raised, away from the nest, mimicking a small rodent (Miller 1951, Oberholser 1974). When predators closely approach or attempt to depredate a nest or fledglings, male and female parents sometimes perform injury-feigning distraction displays, running on the ground dragging one wing and flapping the other conspicuously (Dotson 1971, Dobbs et al. 1998).

Competitors

On their breeding grounds in Colorado, male green-tailed towhees respond to playback of conspecific song only, and they do not respond aggressively to playback of songs of other towhee species, including the sympatric spotted towhee (P.S. Kaplan in Dobbs et al. 1998). Green-tailed towhees do, however, interact aggressively with fox sparrows (*Passerella iliaca*) where the two species breed syntopically (Clark 1932, P.R. Martin personal communication, November 2004). In California's northwestern mountains (Lake County) and in the Sierra Nevada (Fresno County), green-tailed towhees and fox sparrows have overlapping breeding territories and interact aggressively through interspecific chases (P.R. Martin personal communication, November 2004). In Lake County, individuals of each species respond to playback of the other species' song, typically with fox sparrows responding aggressively to green-tailed towhee song, and green-tailed towhees responding subordinately to fox sparrow song (P.R. Martin unpublished data). In Region 2, the green-tailed towhee breeds syntopically with the fox sparrow and a number of other shrub-nesting and ground-foraging species (e.g., Brewer's sparrow in shrubsteppe, Brewer's sparrow and spotted towhee in open pinyon-juniper woodland), and likely competes interspecifically, at some level, for nest sites and/or food resources.

The green-tailed towhee appears to partition nesting habitat with coexisting shrub-nesting passerines, but overlap does occur. In montane chaparral in California, green-tailed towhees tend to nest above ground, either in the center of *Ceanothus* shrubs or *Abies* saplings, or in *Ribes* shrubs in Fresno County, whereas fox sparrows often nest on the ground, typically at borders of *Ceanothus* and *Abies* patches, and never in *Ribes* shrubs (P.R. Martin unpublished data). In northern Arizona, the green-tailed towhee, hermit thrush (*Catharus guttatus*), and MacGillivray's warbler (*Oporornis tolmei*), all of which nest in shrubs in overlapping territories, partition nest microhabitat preferences along a microclimate gradient (Martin 1998). Within each species, nest success is higher at preferred than at non-preferred nest microhabitats, suggesting that preferences are adaptive (Martin 1998).

WEB				CENTRUM
4	3	2	1	

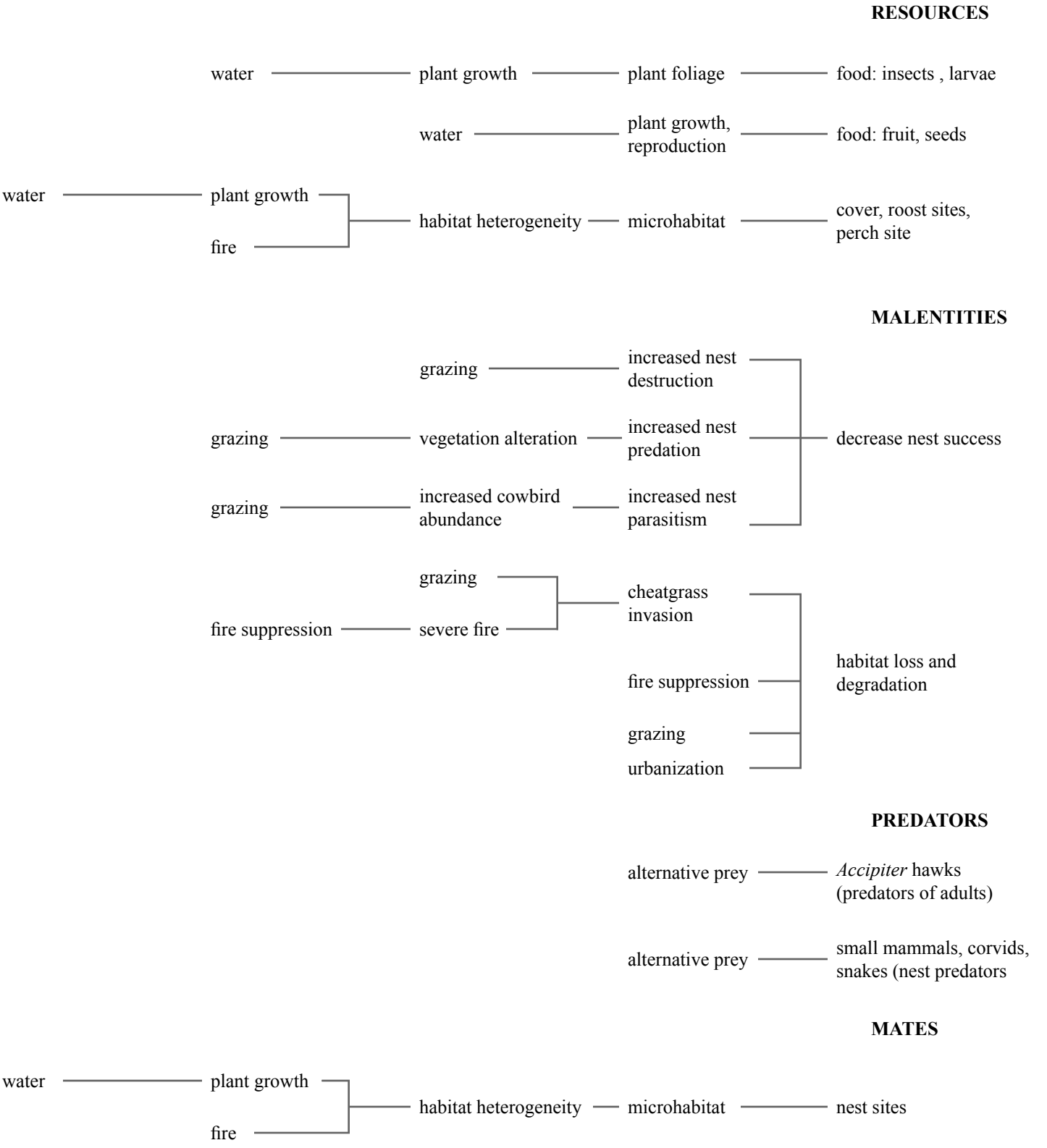

Figure 13. Envirogram outlining ecological relationships of the green-tailed towhee.

Here, the green-tailed towhee appears to partition the habitat with coexisting species and thereby maximize its productivity.

Parasites and diseases

Little information is available on the types of parasites and diseases that affect green-tailed towhees, and no information is available on the frequency and effects of parasitism and infection. Green-tailed towhees host feather mites (*Proctophyllodes* spp.) in California (McClure 1989). Coccidian protozoans (*Isopora* spp.) parasitize cells of the intestinal wall of green-tailed towhees, causing the disease coccidiosis (Herman et al. 1942).

CONSERVATION

Threats

Green-tailed towhees breed in shrub communities characterized by a mosaic of open ground with grasses and forbs, and patches of shrubs, which vary in species richness, density, and vigor. These shrub communities may occur as open shrublands in low-elevation foothills or in mid-elevation basins, or as components of savanna-like habitats in which patches of shrubs occur with scattered trees in ecotones of ponderosa pine or pinyon-juniper woodland. The health and productivity of the species' primary habitats in Region 2, shrubsteppe and montane shrubland, have declined as a result of overgrazing by livestock, fire suppression, the invasion of exotic species, and the interaction of these factors (Saab and Rich 1997, Paige and Ritter 1999, Nicholoff 2003). Additional human activities that threaten green-tailed towhee distribution and productivity by removing, degrading, or fragmenting shrub habitats, include the conversion of shrubland to agriculture, energy development, recreation, and urban development (Beidleman 2000, Nicholoff 2003).

Livestock grazing

Available data suggest that green-tailed towhees are significantly less abundant in grazed habitats than in ungrazed habitats (Saab et al. 1995, Tewksbury et al. 1998). Livestock grazing may negatively affect the breeding success and habitat of the green-tailed towhee in a number of direct and indirect ways. Summer grazing directly threatens the success of nests through the increased risk of physical disturbance or trampling, and indirectly through the increased risk of brood parasitism by cowbirds, or interactive effects of altered vegetation, nest predation, and brood parasitism. That is, via changes to grass, forb, and shrub vegetation, livestock grazing may affect the physical concealment of nests or patterns of parental behavior at nests, which may increase the susceptibility of green-tailed towhees to brood parasitism or nest predation.

Green-tailed towhee populations, however, are most threatened by the long-term effects of grazing on the structure and functioning of shrubland habitats. Habitat alteration of shrublands to increase livestock forage often includes the removal of shrubs, either through herbicide treatment, burning, or mechanical methods, and reseeding with exotic grasses (e.g., crested wheatgrass [*Agropyron cristatum*]) (Braun et al. 1976). Even without direct habitat manipulation, inappropriate grazing indirectly alters the shrub-grass-bare ground mosaic needed by green-tailed towhees. As livestock reduce cover of perennial grasses and forbs, competition for shrubs is relaxed, which allows shrub cover to increase uniformly (Saab et al. 1995, Paige and Ritter 1999), and reduce the mosaic quality of the habitat. Overgrazing facilitates the invasion of non-native annual grasses, which tend to be fire-adapted (Saab et al. 1995, Paige and Ritter 1999). Soil disturbance by livestock also destroys the microbiotic crust (crytogram layer) on the soil surface, which adversely affects water infiltration and nitrogen fixation, increases erosion, and provides safe sites for the germination of invasive non-native grasses (Rotenberry 1998).

Following the establishment of mining and logging activities in the southern Rocky Mountains in the mid-1800's, domestic livestock grazing became a major activity on lands that are now Region 2 national forests. Overgrazing (i.e., grazing too many animals too early in the season and for too long) during the late 1800's and early 1900's contributed to major shifts in the structure, species composition, and fire regimes of forest and grassland/shrub plant communities in Region 2 (Dillon et al. 2003, Meyer et al. 2003, Veblen and Donnegan 2004). Grazing pressure by domestic livestock on Region 2 forests peaked during the 1920's, and habitat-related effects of overgrazing were apparent by the 1930's and 1940's (D. Bradford personal communication, March 2006). Current grazing pressure has decreased over 70% from peak levels and, although grazing practices vary considerably among Region 2 forests and within forests due to specific management situations, grazing is generally rotational and limited to a short period of the growing season (D. Bradford personal communication, March 2006). It is important to note that browsing pressure by native ungulates has increased substantially as livestock grazing pressure has decreased; numbers of deer and elk have increased by

2000% and 4000%, respectively (D. Bradford personal communication, March 2006).

Among habitats important to breeding green-tailed towhees in Region 2, livestock grazing has probably affected shrubsteppe, foothill shrubland, and pinyon-juniper woodland most significantly. By reducing grasses and forbs, and thus competition for tree seedlings, grazing likely improved conditions for seedling establishment, thereby contributing to increases in tree density in pinyon-juniper woodlands and shrub-ponderosa pine savanna, and promoting the invasion of forests into montane grasslands and shrublands (Veblen and Donnegan 2004). Effects of livestock grazing also interact with fire regimes. By reducing fine fuels (i.e., grasses and forbs), livestock grazing also likely contributed to the reduction in fire frequency in low elevation habitats (see below), further promoting tree seedling establishment in shrublands and savannas (Veblen and Donnegan 2004). Heavy livestock grazing in montane grasslands and shrublands may have also promoted the spread of big sagebrush, but it is unclear whether effects were outside the range of natural variation (Meyer et al. 2003). Although sagebrush expansion may have increased shrubland habitat, effects on green-tailed towhees may have been negative if sagebrush expansion was uniform and removed the mosaic quality of the habitat.

Fire suppression

Like grazing, fire suppression has a long history in the western United States and has strongly influenced the present condition and availability of shrubland habitats. Fire suppression in shrubsteppe and montane shrublands produces an increasingly decadent, uniform, dense, and older shrub structure, with little variation in vigor, species diversity, or age structure within a patch (Nicholoff 2003, Knick et al. 2005). In addition to increases in shrub cover, fire suppression allows succession from open shrub communities to conifer-dominated woodlands (Nicholoff 2003). Further, by promoting increased and uniform shrub cover, fire suppression causes shrubland wild fires to be more severe than under natural conditions, a problem that is exacerbated by the invasion of non-native grasses (see below). Because they require remnant patches of live shrubs within burned areas, green-tailed towhees often avoid shrub habitats recently burned by high-severity fires, which typically result in high shrub mortality (McGee 1976, Kerley 1994, Jehle 2004).

Fire suppression in woodland and forest habitats has, to a degree, changed the landscape mosaic of different seral stages that reflect variation in fire frequency and severity (Saab et al. 2005). Green-tailed towhee abundance typically increases following fire in ponderosa pine and mixed-conifer forest, as early successional shrub communities develop in the place of previously closed-canopy forest (Bock et al. 1978, Lowe et al. 1978, Raphael et al. 1987). Hence, fire suppression associated with timber production may result in reduced breeding habitat through (1) the limitation of post-fire successional habitat development (i.e., fire prevention) and (2) the degradation of suitable disturbed forest habitat, via forest succession and fire suppression. In general, fire suppression tends to remove the mosaic quality of shrublands that characterizes green-tailed towhee habitat, at both within-patch and landscape scales.

A policy of fire exclusion during the past century has characterized forest management in Region 2, and this has probably impacted green-tailed towhee populations most significantly by changing the structure of ponderosa and mixed-conifer forests. Fire suppression has caused fire frequency to decline and stand density to increase dramatically in montane and upper montane forests of the Colorado Front Range (Veblen and Lorenz 1991, Veblen et al. 2000, Veblen and Donnegan 2004) and elsewhere in Region 2. A reduction in fuels due to heavy livestock grazing has exacerbated shifts in fire regimes and forest structure (Veblen 2000, Veblen and Donnegan 2004). In the Front Range, and probably in Region 2 in general, historic fire regimes differed with elevation, slope aspect, and forest type. In lower montane ponderosa pine woodland, which is relatively xeric and often includes a strong shrubland component, frequent fires of low-severity maintained open and patchy ponderosa pine woodlands, especially along the southern Front Range (Veblen et al. 2000, Veblen and Donnegan 2004), which are similar to ponderosa pine-fire dynamics in the southwestern United States (Moir et al. 1997, Bock and Block 2005). Fire suppression, which in Region 2 has been most intense in this lower montane zone, has shifted the structure of this habitat type from open, patchy woodland to dense stands of younger ponderosa pine trees. At higher elevations, ponderosa pine forest is more mesic, includes Douglas-fir, and grades into mixed-conifer forest. Here, forest structure was historically shaped by more infrequent, severe stand-replacing fires, which created habitat mosaics of variable seral stages on a landscape scale (Veblen et al. 2000, Veblen and Donnegan 2004). Thus, fire suppression in lower montane ponderosa pine and associated shrub habitats has decreased green-tailed towhee habitat availability by converting shrubland and shrub-ponderosa pine savanna to forest.

Fire suppression in the upper ponderosa pine-mixed conifer zone has decreased green-tailed towhee habitat availability by removing variation in seral stages at a landscape scale.

While fire suppression has probably exacerbated anthropogenic changes to foothill shrubland and pinyon-juniper woodland in Region 2, it has not been as important as livestock grazing in those habitat types (Meyer et al. 2003, Veblen and Donnegan 2004). Although little studied, it is unlikely that fire suppression has greatly altered the fire regimes typical of Gambel oak shrublands and pinyon-juniper woodlands in western Colorado, which were characterized by relatively infrequent, stand-replacing fires (Veblen and Donnegan 2004). Note, however, that as non-native grasses continue to invade foothill shrubland and pinyon-juniper habitats (see below), future effects of fire suppression in those habitats may be very significant.

Introduction of non-native species

The introduction of non-native plants in shrubsteppe, montane shrubland, and pinyon-juniper and ponderosa pine woodland and savanna represents a significant threat to shrubland habitats and, potentially, to green-tailed towhee populations in Region 2. The introduction and spread of cheatgrass (*Bromus tectorum*), in particular, threatens the structure and functioning of the entire sagebrush biome as a result of its life history, competitive ability, and its interaction with fire. By germinating in the autumn, initiating growth early in spring, having a highly efficient shallow root system, and setting abundant seed annually, cheatgrass quickly colonizes and dominates plant communities. Unlike native bunchgrasses, cheatgrass forms continuous dense cover, providing high fuel loads that promote more frequent, larger, more severe, and less complex fires than are allowed by native vegetation. As a result, cheatgrass is rapidly facilitating conversion of shrubsteppe to grassland, especially in Wyoming big sagebrush (*Artemesia tridentata* ssp. *wyomingensis*) communities, from which recovery may not be possible (Rotenberry 1998, Knick et al. 2005).

Conversion of shrubland to agriculture

The conversion of shrubland to agricultural land, either grassland pasture or cropland, not only reduces the amount of shrubland habitat available to green-tailed towhees, but it also degrades adjacent shrubland by aiding the spread of exotic plant species (e.g., Russian thistle [*Salsola kali*]) and facilitating the increase of brood parasites (e.g., cowbirds) and nest predators (e.g., corvids) (Rotenberry 1998). In Region 2, many areas of sagebrush shrubland have been converted to irrigated pastures and orchards (D. Bradford personal communication, March 2006).

Energy development

Energy development and natural resource (e.g., coal, oil, gas) extraction activities directly alter shrubland habitats on the site of operation. Activities associated with energy development, such as the building of roads, pipelines, and powerlines, have significant landscape-level effects of fragmenting habitats, facilitating the spread of invasive species, and facilitating the increase of nest predators (e.g., corvids along powerlines) (summarized by Knick et al. 2003). In Wyoming, existing oil and gas wells are located mainly in sagebrush-dominated habitats (Knick et al. 2003). In Colorado, development of coalbed methane reserves is likely to increase on at least one national forest (San Juan National Forest), primarily in sagebrush, montane shrubland, and ponderosa pine habitats; this could affect green-tailed towhee populations negatively through loss or fragmentation of habitat or increases in nest predators (Ecosphere Environmental Services 2004).

Recreation

Recreation in the form of off-road vehicle (ORV) activity away from established roads and trails represents a threat to green-tailed towhees and their shrubland habitats. Off-road vehicle activity increases physical damage to vegetation and the soil surface, which increases mortality risks to birds and their nests and causes erosion. Further, the creation of roads and trails for ORV recreation (or other purposes) allows improved access to shrubland habitats, where off-trail recreation may damage previously inaccessible shrublands. Additional road building also further fragments shrubland habitats and facilitates the spread of exotic species. Because the shrubland habitat preferred by green-tailed towhees typically is not concentrated along watercourses or other formations that concentrate human activity, low impact recreational activities (e.g., birdwatching) in shrubland habitats are unlikely to have any effect on green-tailed towhee abundance or productivity. In fact, experimental work shows that low levels of human intrusion do not affect green-tailed towhee abundance in subalpine environments (Gutzwiller and Anderson 1999).

Urban development

Shrubland and pinyon-juniper woodland in the foothills along Colorado's Front Range, where much of the land is privately owned, is increasingly at risk of urban development (e.g., housing) as the human population increases. Urbanization changes avian habitat and food supply, predator and competitor communities, and potentially the demography of a species. Urban development leads to the alteration of natural fire regimes and the depletion of streams, alters nutrient cycling, removes natural vegetation, fragments remaining habitat, introduces exotic predators and competitors, and facilitates the increase of natural predators (Marzluff et al. 1998). While all of these factors may impact green-tailed towhees or their habitats, research investigating these factors has not been conducted.

Conservation Status of the Green-tailed Towhee in Region 2

Green-tailed towhee populations are considered secure range-wide and within Region 2 states that have breeding populations (i.e., Wyoming and Colorado; NatureServe 2004). Within Region 2, the green-tailed towhee is a MIS on the San Juan National Forest (Ecosphere Environmental Services 2004) and a priority species in the Colorado bird conservation plan (Beidleman 2000). The species is considered a priority in Colorado because it is closely associated with montane shrubland habitat; due to the species' high abundance in the state, Colorado holds a high responsibility for its conservation.

Although the green-tailed towhee is not rapidly declining or imminently threatened in Region 2, its conservation merits long-term attention due to its relatively specific habitat requirements and current threats to those habitats. The species breeds primarily in montane shrubland in Colorado (**Figure 11**, Righter 1998), but likely uses shrubsteppe to a large degree in Wyoming, where shrubsteppe is much more widespread than in Colorado (Knick et al. 2003). Both of these habitats are experiencing severe degradation and fragmentation due to livestock grazing, invasion of exotic grasses, and fire suppression, to the point where the shrubsteppe ecosystem is at risk of large-scale collapse (Knick et al. 2003).

While data suggest that populations are stable range-wide, including within Region 2, population trend data carry a significant degree of uncertainty in many areas, including portions of Region 2. More importantly, there is very little information available on the demography of green-tailed towhee populations anywhere in the species' range. Measures of abundance or density, on which population trend data are based, do not necessarily reflect habitat quality with respect to survival and reproduction (Van Horne 1983), and thus they do not address the potential problem of source-sink population dynamics (Pulliam 1988) among habitats or geographic areas used by green-tailed towhees. There currently are very few data available on which to base conjecture regarding variation in productivity among different habitats or management practices. For example, although reproductive success appears to be lower in disturbed areas of coniferous forest (Arizona) than in shrubsteppe or montane shrubland communities (Colorado; **Table 8**), this may be an effect of variation in the species' life history at the edge of its range versus the center of its range, where it may be better adapted to ecological conditions (Jehle 2004).

Lack of information notwithstanding, the loss, degradation, and fragmentation of montane shrubland habitat in Colorado and Wyoming, and shrubsteppe habitat in Wyoming, will likely have the strongest negative impacts on green-tailed towhee populations in Region 2. Any land use or management activities that remove large areas of shrubs without leaving a mosaic of reasonable shrub cover (e.g., inappropriate grazing regimes), or that prevent natural habitat disturbance and recovery (e.g., fire suppression, overgrazing) will likely impact green-tailed towhees negatively in Region 2.

Potential Management of the Green-tailed Towhee in Region 2

Implications and potential conservation elements

Little information is available on how management practices influence green-tailed towhee populations specifically. Nevertheless, in shrubsteppe and montane shrubland communities, the most important management considerations for the green-tailed towhee probably are the maintenance of habitat heterogeneity, with respect to species composition, vigor, cover, and age structure of shrubs, and the prevention of invasion by non-native annual grasses (e.g., cheatgrass). Toward this goal, management of shrublands should attempt to restore natural disturbance regimes and to minimize unnaturally high levels of habitat alteration at a landscape scale. Thus, fire management and livestock grazing should be of primary concern to land managers seeking to maintain or restore healthy green-tailed towhee populations. Habitat alteration to increase livestock

forage (e.g., removal of shrubs, planting of non-native grasses) and indirect habitat alteration resulting from grazing itself (e.g., increased shrub cover, decreased native grass and forb cover) likely have negative effects on green-tailed towhee abundance and distribution, and possibly survival and productivity. Wildfire, a natural disturbance agent that maintains green-tailed towhee habitat at multiple spatial scales, may negatively affect green-tailed towhee abundance and distribution where effects of fire suppression, livestock grazing, and invasion of exotic species increase fire severity (e.g., due to higher fuel loads from increased cover of shrubs, young trees, and non-native grasses).

Prescribed fire is an important tool in habitat management, but its effects on green-tailed towhees and their habitat may vary with other land management practices. In Rocky Mountain National Park, Colorado, for example, elk (*Cervus elaphus*) herbivory is very high in montane shrubland and may decrease the post-fire regeneration of shrubs, and thereby decrease the long-term suitability of the habitat for green-tailed towhees (Jehle 2004). In general, and in addition to current levels of herbivory by native ungulates or livestock, green-tailed towhee response to fire depends on fire severity, time necessary for post-fire shrub regeneration, and the presence and size of unburned remnant patches within the burned area. Following prescribed fires in shrubsteppe and montane shrubland habitats, green-tailed towhees may persist on burned areas if sufficient patches of unburned shrubs remain intact, but they may be absent or occur at very low densities for up to eight years on severely burned areas (McGee 1976, Kerley 1994, Jehle 2004).

In closed-canopy forest landscapes, fire suppression reduces habitat availability for green-tailed towhees by preventing the natural disturbance and subsequent development of successional habitats. In California's Sierra Nevada, green-tailed towhees colonize post-fire areas within five years and maintain breeding populations in the successional habitat for over 25 years (Bock and Lynch 1970, Bock et al. 1978, Raphael et al. 1987). Similar results have been found following wildfire in ponderosa pine forest in Arizona (Lowe et al. 1978). Prescribed fire represents an important tool to restore and maintain the mosaics of shrub, grass, and bare ground that are preferred by green-tailed towhees at the within-patch scale in lower montane forest. Relaxed fire suppression, however, will be necessary to restore the shifting mosaic of young post-fire seral stages available to green-tailed towhees at the landscape scale in mid-elevation ponderosa pine and mixed-conifer forest. The lack of variable post-fire seral stages in mid-elevation forest due to fire suppression may be partially offset by timber harvesting in some areas. Again, few data are available regarding the response of green-tailed towhees to management practices, but one study found the species to colonize an area, formerly comprised of virgin mixed-coniferous forest, one to two years after moderate-heavy removal of the overstory through timber harvest (Franzreb and Ohmart 1978). Timber management practices that remove large areas of canopy cover, sufficient for the development of diverse shrub communities, may benefit green-tailed towhee populations, but further research is necessary to understand the most effective management approaches.

Tree density in pinyon-juniper woodland has increased as a result of fire suppression and livestock grazing, thus removing or reducing the pre-settlement savanna-like quality of that habitat. Mechanical removal of pinyon and juniper trees may improve green-tailed towhee habitat. In pinyon-juniper woodland in Rio Blano County, Colorado, the number of green-tailed towhee territories per 10 ha increased from zero in unchained areas to 4.4 and 3.8 in chained areas 8 and 15 years following chaining, respectively (O'Meara et al. 1981). Green-tailed towhees were also more common in chained than unchained pinyon-juniper woodland in northwestern Colorado (Sedgwick 1987).

Tools and practices

Species inventory and population monitoring

Numerous standardized methods have been developed to survey (i.e., determine the presence and abundance of) bird species and to monitor their populations (i.e., through repeated surveys) over time and/or space. The most widely used techniques in landbird studies are index count techniques (e.g., point counts), in which counts (i.e., detections) of individual birds are recorded during one or more surveys of points, transects, or other defined areas (Ralph et al. 1995, Rosenstock et al. 2002). Recently, the reliability of index count techniques has been questioned because of fundamental assumptions that fail to consider variation in detection rates (i.e., that the number of individuals detected represents a constant proportion of the actual number of individuals over space and time) (e.g., Nichols et al. 2000).

Due to the constraints associated with traditional index counting, a suite of robust new techniques has been developed that take detectability issues into consideration. Distance sampling, in particular line

transect distance sampling, is one such technique that uses the basic field methodology of traditional line transect point counts, except that the observer estimates the horizontal distance from the transect to each bird seen or heard during the count. The distance sampling technique assumes that all birds on or near the transect are detected, that birds do not move in response to the observer prior to detection, and that distances are estimated accurately (Rosenstock et al. 2002).

Distance sampling is one of the most robust techniques available and currently is being used in large-scale and long-term monitoring programs within Region 2. Both the MCB and the Monitoring Wyoming's Birds (MWB) projects, originated and administered by RMBO, use line transect distance sampling to monitor breeding bird populations on a randomly allocated and habitat-stratified basis (Leukering et al. 2000). Although inventory and population monitoring methodology has not been developed specifically for the green-tailed towhee, the species is a priority species in Colorado's PIF bird conservation plan and thus is a focal species of the MCB project. Any agency developing a green-tailed towhee survey or monitoring program should consider adopting the methods of MCB so that data collected by each organization are directly comparable.

In addition to count-based monitoring programs, which indicate if a population is increasing, decreasing, or stable, field research on population demography provides the data (e.g., survival, productivity) necessary to infer the reasons that drive changes in abundance. Demographic field techniques of constant-effort banding and nest monitoring provide data on survival (e.g., through capture-recapture methods) and productivity (e.g., clutch size, nest success), respectively. These data are critical in constructing demographic models, which are powerful tools to assess population viability, identify conservation priorities, and evaluate the effectiveness of management efforts. Long-term demographic projects contain standardized protocols for nest monitoring (BBIRD; Martin and Geupel 1993, Martin et al. 1997) and banding (MAPS; DeSante et al. 1995). An integrated approach to population monitoring, comprised of population trend and demographic field research, will provide the most comprehensive information on population change and necessary elements of conservation strategies (DeSante and Rosenberg 1998).

Habitat inventory and monitoring

The green-tailed towhee is a common species that is characteristic of montane shrubland habitats in Region 2. Because green-tailed towhees prefer shrubland habitats characterized by variation in plant species diversity, physical properties, and age structure, variation in green-tailed towhee abundance likely indicates variation in the effectiveness of natural processes to maintain shrublands in a natural state, and thus reflects an index of environmental health. Further, green-tailed towhees are conspicuous and easily detectable early in the breeding season, when males are singing at high rates. For these reasons, the green-tailed towhee represents an ideal management indicator species for montane shrubland and associated habitats in Region 2.

Relationships among population trends and demographic data in the context of habitat quality and structure, habitat variation and change, and habitat management practices are necessary for identifying conservation issues and developing appropriate conservation strategies. As such, habitat inventory and monitoring data are critical to interpreting results of population and demographic studies, and understanding their conservation implications.

There are no existing protocols for the inventory and monitoring of green-tailed towhee habitat. Nevertheless, given what we know about this species' biology and habitat use, habitat sampling should focus on (1) the spatial distribution of shrubs and patches of shrubs, (2) variation in the spatial distribution of shrub species diversity, shrub cover, shrub density, shrub vigor, and shrub age class, and (3) density and spatial distribution of trees and associated canopy cover. Vegetation should be sampled at multiple spatial scales, including the nesting or foraging site, patch, and landscape. The BBIRD protocol (Martin et al. 1997) provides standardized techniques for sampling vegetation in the context of bird habitat at multiple spatial scales.

Management approaches

Few management recommendations have been developed specifically for the green-tailed towhee. Within Region 2, Beidleman (2000) generally outlines management issues and recommendations for the species in Colorado. A number of other plans provide habitat-based, as opposed to species-specific, management recommendations that are relevant to the green-tailed towhee. Within Region 2, the Wyoming bird conservation plan provides habitat management recommendations for bird communities inhabiting shrubsteppe and mountain foothills shrub habitats (Nicholoff 2003), which represent those most important

to green-tailed towhees in Wyoming. In addition, Paige and Ritter (1999) provide detailed management goals and recommendations for shrubsteppe birds, including the green-tailed towhee, throughout the Intermountain West. These community-level approaches represent the most appropriate management strategies since many species are potentially at risk from the same threats, which are manifest primarily through the degradation of habitat functioning. These conservation plans utilize management tools already available to land managers in Region 2, encourage management that is both consistent with natural disturbance regimes (e.g., fire), and integrate current land use practices with conservation needs of native birds. Below, I summarize management approaches relevant to Region 2, outlined in PIF state plans (Beidleman 2000, Nicholoff 2003) and a shrubsteppe habitat report (Paige and Ritter 1999), to achieve healthy shrubland ecosystems and green-tailed towhee populations.

General: The most important conservation approach for green-tailed towhees is the maintenance of a mosaic of native grasses and forbs, and shrubs with variable cover, species composition, and age structure. To this end, public land managers and private landowners should provide a landscape mosaic of different structural stages of shrub habitat. Land managers should strive for a no-net-loss of shrubsteppe and montane shrubland habitat, an approach that does not seek to preclude current land use and management, but rather uses mitigation to offset habitat loss or degradation through restoration or conservation elsewhere. Achieving this goal requires careful management of activities that tend to remove, reduce, or fragment shrub habitats (e.g., ORV travel, road building, urbanization, natural resource extraction).

Grazing: Proper stocking levels and grazing regimes can be effective management tools in the conservation of shrub habitats, but land managers should also consider browsing pressure by native ungulates when determining appropriate grazing practices. In general, appropriate livestock grazing allows shrublands to achieve climax successional stages and produces a heterogeneous landscape of variable shrub patches. Specific livestock management considerations that will benefit green-tailed towhees include rotating stock to avoid green-tailed towhee breeding areas during the nesting season, minimizing stock concentrations within sites, rotating livestock use of sites between years, and keeping livestock off post-fire sites until native grasses become established.

Fire: If implemented properly, the re-establishment of fire allows the maintenance and restoration of the heterogeneous landscape critical for green-tailed towhees. Prescribed burns that are small in scale, produce a patchy burn, and leave areas of unburned vegetation are optimal for green-tailed towhees. To minimize erosion, cheatgrass invasion, unwanted damage to plants, and nest failure, prescribed burning should be performed in late fall or early spring, when plants are dormant and birds are not breeding. Again, keeping livestock off post-fire areas until native grasses are established prevents damage to soil and native perennials, invasion by non-native grasses, and reduces recovery time of shrubs.

Information Needs

The natural history of the green-tailed towhee remains poorly known throughout its range, in part due to its particularly secretive nature. As a result, there are large gaps in our knowledge of its habitat selection, breeding biology, population biology, and community ecology. Of primary importance, we need more information on habitat use and demography, especially survival, from across the species' range and from both breeding and non-breeding seasons.

Within Region 2, the breeding distribution of the green-tailed towhee is well understood in Colorado, based on extensive field surveys conducted for the Colorado Breeding Bird Atlas. RMBO's Monitoring Colorado's Birds project currently provides information on the species' relative abundance and density in various habitat types, and it will eventually also yield high-quality data on population trends in Colorado. While the Monitoring Wyoming's Birds project is starting to provide similar data for Wyoming, our understanding of the species' distribution, habitat use, and population density remains relatively rudimentary in that state. Habitat-specific data on distribution and relative abundance are still badly needed for Wyoming. As distribution, habitat use, and population density data become more and more available, largely as a result of these monitoring projects, our ability to critically evaluate conservation needs and to develop conservation strategies for the green-tailed towhee in Region 2 will improve.

To fully understand the ecological and conservation implications of the population status and trend data being produced (see above), we need breeding season demographic data (i.e., reproductive

success, survival) from different types of shrub habitats on a landscape scale. Two recent studies in Colorado have dramatically added to our knowledge of green-tailed towhee reproductive success, with respect to Region 2-specific habitat types and in general. Similar research remains unavailable for Wyoming, where it is badly needed. To understand how land management practices (e.g., grazing, fire suppression, prescribed fire) affect green-tailed towhee breeding populations, we need well-designed experimental studies, with adequate spatial and temporal replication, to examine effects of various management practices on the species' distribution, habitat use, and reproductive success. For instance, despite the importance of fire in western ecosystems and limited evidence that fire creates and maintains green-tailed towhee habitat, no published study reports the species' response to fire in the central or southern Rocky Mountains (Saab et al. 2005). Similarly, the impact of grazing on green-tailed towhees is largely unknown, yet it represents one of the greatest research needs in Region 2. For all practical purposes, regardless of the management issue, we need to understand the minimum and optimum shrub cover and habitat area required to sustain productive populations. In addition to research directed at management effects on green-tailed towhee breeding populations, we need information on how the birds respond to threats in general. In particular, how vulnerable are green-tailed towhees to mining, oil and gas development, recreation, and urban development? How do habitat degradation and fragmentation resulting from those activities affect green-tailed towhee reproductive success and site fidelity, and are there thresholds above which reproductive success or site fidelity declines?

In addition to breeding, green-tailed towhees spend significant amounts of time in Region 2 during migration each spring and fall, at which time stopover habitat may be very important. Recent work suggests that the majority of mortality in migratory songbird populations occurs during the migratory periods (Sillett and Holmes 2002), yet virtually nothing is known about green-tailed towhee ecology and behavior during migratory stopover in Region 2. Research directed at identifying habitat relationships and the factors that influence habitat quality for green-tailed towhees during migratory stopover in Region 2 would be very useful.

DEFINITIONS

BBIRD – Breeding Biology Research and Monitoring Database; initiated and maintained by the Montana Wildlife Research Cooperative Unit at the University of Montana in Missoula, this database consists of breeding biology data (clutch size, nest success, brood parasitism) collected by standard methods at numerous sites in North America.

CNRCP – Cornell Nest Record Card Program; a program organized by the Cornell Lab of Ornithology in Ithaca, New York that archives nest records and associated data (e.g., nest location, nest contents) collected by volunteers throughout North America.

RMBO – Rocky Mountain Bird Observatory; a nonprofit organization based in Brighton, Colorado that seeks to conserve Rocky Mountain and Great Plains birds through research and education outreach.

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